1971

The Annual Net Primary Production and Decomposition of the Salt Marsh Grass, Spartina Alterniflora, Loisel. In the Barataria Bay Estuary of Louisiana.

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THE ANNUAL NET PRIMARY PRODUCTION AND DECOMPOSITION OF THE SALT MARSH GRASS *Spartina alterniflora* Loisel. IN THE BARATARIA BAY ESTUARY OF LOUISIANA

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Botany

by
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B.S., University of Southwestern Louisiana, 1964
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December, 1971

ACKNOWLEDGEMENT

The author wishes to express his appreciation and gratitude to Dr. James G. Gosselink whose inspiration and guidance made this paper possible. His sincere appreciation is extended to Dr. William G. Smith for his suggestions and advice on the study. Thanks are also extended to Drs. Bert Wilkins, Jr., John Baker, and Charles Schexnayder for their constructive criticism.

The author owes a particular debt of gratitude to Mr. Richard Condrey for his suggestions and criticism of certain aspects of the research. Appreciation is extended to Mr. Donald Schlatre for his help with computer calculations, and to Mr. Wilmer Stowe and all others who were instrumental in sampling assistance.

The author wishes to express his sincere thanks for financial assistance given by the Louisiana State University Sea Grant Program which is maintained by the National Oceanic and Atmospheric Administration of the U. S. Department of Commerce.

To his wife, Wanda, the author expresses his profound gratitude for her constant encouragement and understanding in the past several years.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

FIGURE Page

ABSTRACT

The annual net primary production of Spartina alterniflora was determined for both inland and streamside marsh. Production was initially calculated by summation of the monthly changes in standing crop; however, an alternate method is suggested which measures production as a dynamic process, and accounts for certain inherent discrepancies which occur in the initial method. The alternate method which is termed "true net production" was found to approximately double the production calculated by summation of the monthly change in standing crop. The two methods are compared and discussed.

The rates of decomposition and loss of dead standing Spartina from the marsh were examined by utilizing nylon mesh litterbags. The streamside marsh, inland marsh, and a tidal channel were considered in the measurement of loss rates. Dead material was found to decompose most rapidly in the tidal channel in which the bags were constantly submerged, followed in order by the streamside marsh and inland marsh.

The decomposition rates of four particle size fractions of dead Spartina, considered small enough to have been easily washed off the marsh surface, were studied under laboratory conditions. At a constant temperature of 30C particles of 111 microns or less were completely decomposed in 30 days, whereas those larger than 111 microns were more slowly affected.

The net primary production and decomposition of Spartina alterniflora are discussed as a dynamic process. Several parameters of this process have been examined experimentally, and several others have been suggested as speculation.

INTRODUCTION

Coastal salt marshes are rather unique ecosystems representing a transition between the terrestrial and aquatic habitats. These shallow water estuarine systems usually exhibit a low diversity with high numbers of organisms. Practically all net primary production results from salt tolerant marsh grasses which are consequently the primary contributors of organic matter to the detrital food chain. Nearly all primary consumers are aquatic with only small quantities of primary production actually removed by grazing.

Description of the Study Area

Barataria Bay is a vast shallow water estuarine system bounded on the east by the Mississippi River and on the west by Bayou Lafourche. All of the lower part of this system is affected by daily tides which may be wind influenced. Although linear amplitude is only about 50 cm, tides are higher in spring and summer when south winds predominate and lower in winter when north winds occur. Tidal waters seldom cover the marsh in winter; however, spring and summer tides may be 30 to 60 cm higher, and completely inundate the marsh daily. Temperatures vary from slightly above 30C in the summer to approximately 10C in winter.

The dominant vegetation in the southern marsh area is Spartina alterniflora Loisel. which is the primary contributor of organic matter to the detrital food chain. Where salinity is usually over 20 parts per thousand, Spartina alterniflora occurs in distinct ecological zones in nearly pure stands. Occasionally species such as Spartina patens,

Distichlis spicata, Salicornia virginica, and Juncus romerianus are found intermixed. However, these minor species constitute only a small percentage of the total vegetation.

The area selected for the measurement of primary net production and decomposition of Spartina is located near Airplane Lake (Figure 1) which is in the southern region of Barataria Bay. Streamside marsh (1), inland marsh (2) and a tidal channel (3) draining Airplane Lake were considered in this study.

The Net Production and Decomposition of Spartina

The net primary production and decomposition of Spartina alterniflora is a dynamic process involving a number of physical and biological factors. However, production estimates have only been determined either by measuring peak standing crop or changes in live and dead standing crop (Smalley 1958). Neither of these methods is adequate as they do not account for considerable quantities of material lost either before peak standing crop is reached or between monthly sampling periods. Decomposition studies have been limited primarily to measurements of loss from litterbags or estimates of detritus abundance (Odum and de la Cruz 1967).

This study was undertaken in an effort to determine the net production and decomposition of Spartina. Specific objectives were:

1. The measurement of net production according to changes in monthly standing crops for both inland and streamside marsh.
2. The measurement of decomposition rate of Spartina in litterbags placed in the marsh.

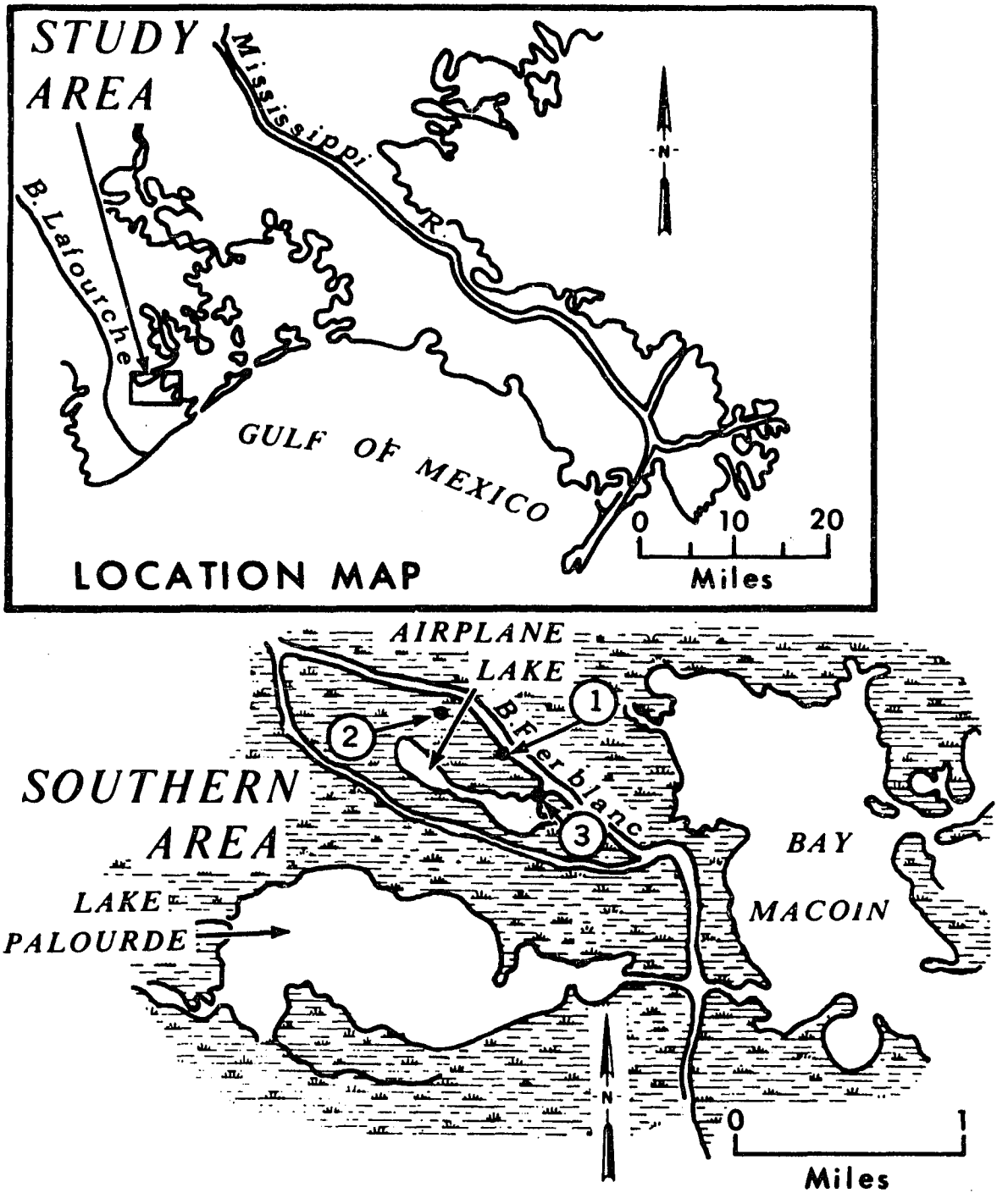

Figure 1. Location map of the southern Barataria Bay estuary indicating the sample locations near Airplane Lake.

Since discrepancies were noted in the measurement of net production by change in standing crop, a method utilized by Wiegert and Evans (1964) to measure production of a grassland ecosystem is suggested.

The study was further expanded to examine the rates of decomposition of detritus particles which were considered small enough to be easily washed off the marsh surface.

REVIEW OF LITERATURE

I. METHODS OF MEASUREMENT OF PRIMARY PRODUCTION

A. Aboveground Production

The net production of vascular plant communties has characteristically been estimated by clipping the aboveground vegetation, most often a single clipping at peak standing crop. Belowground production has been ignored, primarily because of the difficulty involved in collecting and making reasonably accurate estimations of the biomass. The establishment of accurate methods in determining primary production is most important to the study of salt marsh ecology. Lewis (1970) has reviewed the various methods and classifies them into four categories; the gas exchange method, growth analysis, Allen curve analysis, and frequent harvest methods. Of these four, growth analysis and Allen curve analysis are not frequently utilized and will not be discussed.

1. Gas Exchange Method

Various adaptations of the gas exchange method are employed, but all involve the differential measurement of photosynthetic carbon dioxide uptake within a closed canopy.

a. Single Leaf Approach

The single leaf method has been utilized by Alexander and McCloud (1962) and Brun and Cooper (1967) who enclosed a single leaf within a chamber and determined the rate of carbon dioxide uptake either by absorption in soda lime or with an infrared gas analyzer. Total

production within an area can be determined by multiplying the production of a single leaf by the number of leaves per unit area.

b. Whole Canopy Approach

Measurement of a number of individual plants has been achieved by enclosing an area of vegetation within a clear plastic canopy and drawing outside air across this sample plot (Musgrave and Moss 1961, Alexander and McCloud 1962, Baker 1965, Pearce, et al. 1965, and Brun and Cooper 1967). An infrared analyzer is used in differentially analyzing inflowing and outflowing air. The reduction of carbon dioxide is used to calculate production rates. Respiration within the canopy is accounted for by measuring carbon dioxide concentration for short periods within an opaque or darkened canopy.

c. Open Field Approach

Open field measurements of carbon dioxide uptake have been attempted (Monteith 1962) by measuring carbon dioxide flux at varying levels within and above the vegetation. The net carbon dioxide assimilation minus plant and soil respiration result in a carbon dioxide balance from which production can be calculated.

2. Harvest Methods

Peak standing crop determinations are not used to any extent, as they grossly underestimate production (Odum 1960, Malone 1968). A stand of vegetation usually matures over an extended time period, hence dying and dead material are not accounted for. A variety of frequent harvest methods have become most widely accepted, as they do account for most of the dead and dying material within the growing season. Harvest methods are also most feasible economically, as expensive instrumentation is not required.

Although frequent harvest methods do reduce the error due to constant mortality, they may also grossly underestimate net production, particularly in ecosystems where considerable amounts of plant material are lost between sampling intervals. Ecosystems in which a high rate of plant removal by herbivores occurs, or in coastal marshes subject to tidal flushing, are most susceptable to loss between sampling intervals.

a. Wiegert-Evans Method

Wiegert and Evans (1964) have established a method which attempts to rectify this situation by estimating net primary production by summation of the changes in standing crop while accounting for disappearance plus mortality. Changes in standing crop of live and dead vegetation is determined by the clip method, and the rate of disappearance of dead material by a "paired-plots" method or by litterbag loss.

Wiegert and Evans found that the paired-plot method gave higher net production values than the litterbag method due to lower decomposition rates in the litterbags. They attributed the lower rates in the litterbags to the restriction of scavengers and decomposers, or the prevention of natural contact with the decomposed material on the surface.

b. Polish Modification of Wiegert-Evans Method

Lomnicki, et al, (1968) have suggested a simplified procedure which eliminates the paired-plots of Wiegert and Evans. All dead material is removed from a plot at time t_0, and both live and dead material collected at time t_1. The amount of dead material collected at time t_1 is considered to be the dead materials accumulated within

the time interval (t_1-t_0), and the live material collected as live standing crop at t_1. This live standing crop value is used as the starting live biomass (b_0) for the next time interval. One additional plot is required at time (t_0) to determine the live standing crop in order to measure live production in the interval t_1-t_0, but only one plot is required thereafter. Production for a time interval is thus equal to the sum of the live production (b_1-b_0) and the mortality of live or accumulation of dead material (t_1-t_0).

The Wiegert-Evans method requires that three basic assumptions be met: (1) the rates of disappearance from the two quadrats must be equal, (2) the biomass and species composition of the dead material on the two quadrats must be identical, and (3) no addition to the dead material of the second plot is made during the interval between samplings. Lewis (1970) feels that assumption one and two require precise pairing of the plots, which is difficult in heterogenous vegetation. Assumption three requires a short sampling period.

Two assumptions are inherent in the Lomnicki method. First, the presence or absence of dead vegetation does not influence the mortality rate of live vegetation, and second, the sampling interval must be short enough to prevent a loss of material that has died in the time interval.

Lewis has proposed a "balance sheet" method which would show all of the compartment transfers of net production. The equation proposed is : $P_{Ni} = P_{Gi} - (R_{Ai} + R_{Bi}) = AA_i + AB_i = NPP_i$ or net photosynthesis (P_{Ni}) equals gross photosynthesis (P_{Gi}) minus respiration aboveground (R_{Ai}) and belowground (R_{Bi}), which is equal to the net aboveground (AA_i) and belowground assimilation (AB_i) which is the net primary production (NPP_i) for time interval i.

Lewis suggests that the best method for determining net primary production will be a combination of the balance sheet method and the calculation of turnover rates for belowground plant material.

B. Belowground Production

A variety of methods have been attempted to measure belowground productivity; however, all have proven to be time consuming and not very reliable. Not only is it difficult to separate roots from soil, but also to distinguish living from dead roots.

Dahlman and Kucera (1965) were somewhat successful in separating roots of prairie grass from soil by soaking core samples in a one percent Calgon solution for an hour, and then oxidizing any remaining soil in a 0.8% solution of sodium hypochlorite. Highest root production occurred from April to July, and they estimated that twenty-five percent of the root system was replaced per year. Four years would thus be required for a complete turnover.

Ueno, et al. (1967) distinguished living root systems by applying carbon-14 to the aboveground portion and using autoradiograph techniques on the roots. This method was successful, but proved to be time consuming and limited in its usefulness.

The ratio of belowground to aboveground production has been found to vary with the seasons, the age of the plants, and the amount of moisture in which the plants were growing (Bray 1963). Mutoh, et al. (1968) reported that the biomass of underground parts of a Miscanthus community showed seasonal changes in close relation to the seasonal changes of aerial parts.

Westlake (1966) studied the relation of aboveground to belowground production of Glyceria, and noted that the percent of underground to aboveground growth varied with the season with 85% of the biomass underground in winter and 40% in summer.

II. PRIMARY NET PRODUCTION OF SALT MARSHES

Chapman (1960) describes salt marshes as areas of land which border the coast, which are dominated by salt tolerant grasses, and are subject to tidal inundation. He classified these marshes from New Jersey to Louisiana as coastal plain type.

The dominant vegetation of the Louisiana coastal marshes is Spartina alterniflora Loisel. which occurs in salinities over twenty parts per thousand, in distinct ecological zones in nearly pure stands. According to O'Neil (1949) the highly saline marsh from near Leeville, Louisiana, to the Gulf of Mexico supports the most extensive area of practically solid stands of Spartina alterniflora found on the Gulf coast.

Two distinct height forms are noted in the Louisiana marshes with tall Spartina growing on the stream banks, rather abruptly grading to short Spartina in the inland areas. Stroud and Cooper (1968) and Marshall (1970 a,b) considered three zones in a North Carolina marsh; however, others consider only two (Smalley 1958, Morgan 1961, Udel, et. al. 1969, and Williams and Murdoch 1969).

Determination of the net primary production of Spartina has been accomplished only through the harvest method, with several means of determining net production utilized. Williams and Murdoch estimated net production through peak standing crop determination, whereas Morgan

attempted a figure by determining peak live standing crop and adding the increase in dead material over the summer months. Smalley devised a method of determining production which proved to be considerably more accurate, as it accounted for the death of live material between sampling periods and before a peak standing crop is reached. He used several criteria:

1. If, between sampling periods, there is both an increase in the standing crop of living Spartina and an increase in the standing crop of dead Spartina, then net production is the sum of the increases.
2. If both living and dead standing crop decrease, then production is zero.
3. If the standing crop of living Spartina increased, and the standing crop of dead Spartina decreased, production is equal to the increase in living material.
4. If the amount of dead Spartina increases and the amount of living decreases, they are to be added algebraically; if the result is negative, production is zero; if the result is positive, the resulting figure is equal to production.

Stroud and Cooper compared Smalley's method which measures change in standing crop with the peak standing crop method, and found that the latter underestimated net production by approximately twenty-five percent.

Smalley measured net production of Spartina in the Georgia salt marshes by periodically harvesting the standing crop of grass. The grass was clipped at mud level from 0.1 square meter quadrants ten meters apart along a transect, and the living and dead grass were

separated and oven-dried. Annual production of the short Spartina amounted to 643 grams dry matter per square meter while tall Spartina production was 1098. Average production of the entire marsh was 973 grams per square meter based on estimates of production of short and tall Spartina in proportion to the area occupied by each.

Morgan estimated the annual net production of Spartina in the Delaware Bay estuary to be 445 grams dry matter per square meter.

Stroud and Cooper determined annual net Spartina production in a North Carolina estuary by clipping 0.1 meter square plots at either monthly or bimonthly intervals. Short Spartina production was 329 grams dry matter per square meter, medium 461, and tall 1296.

Udel, et al. measured productivity in a New York salt marsh by harvesting plants from square meter plots in selected representative locations. Determination of total production within the estuary was made by estimating the distribution of grass species by planimetry of color aerial photographs. Production for short Spartina marsh was 508 grams per square meter, and 827 for tall grass.

Williams and Murdoch estimated net production of Spartina in the Beaufort, North Carolina area by peak standing crop. One square meter quadrats were clipped at five week intervals at each of ten locations. Annual production for the entire marsh was calculated to be 650 grams dry material per square meter.

Production is evidently greater in the more southerly marshes which is consistent with our data, as our production values are higher than any recorded to date when calculated on the same basis. It must be emphasized that none of the methods utilized in calculating the

annual production of Spartina accounts for material lost by tidal flushing between sampling intervals.

III. ORGANIC DETRITUS

The importance of organic detritus in the food web of the aquatic environment has been well established. Darnell (1967 a) suggested that organic detritus includes all types of organic material in various stages of microbial decomposition which represent potential energy sources for consumer species. Particulate detritus is defined as material greater than one micron in diameter, and subparticulate as less than one micron in diameter.

Odum (1962) suggests energy flow models in which net primary production is utilized either through grazing food chains or detritus food chains. Odum and de la Cruz (1963) concluded that most of secondary energy flow follows the detritus food chain in "detritus type" ecosystems such as estuaries. They suggest that this type of energy flow pattern permits the development and maintenance of a large organic structure within the community, which provides a stable habitat for a greater diversity of organisms than in a grazing energy flow pattern.

Darnell (1961, 1964, 1967 b) has found that particulate organic detritus is ingested in quantity by zooplankton, fishes and benthic invertebrates, and that areas of zooplankton are associated with detritus abundance and not phytoplankton abundance. He suggested that organic detritus represents a major storage, transport, and buffer mechanism for the estuarine ecosystem as: (1) organic matter produced in a growing season may be released at a later time, (2) detritus can

be transported considerable distances from the point of production, and (3) availability of detritus in food chains continues during seasons of low primary production.

Minshall (1967) measured the quantity of detritus in a woodland springbrook community, and suggests that suspended particulate, attached particulate, and allochthonous leaf material are the chief potential sources of food in the community.

W. E. Odum (1971) suggested that vascular plant detritus originating from red mangrove leaves serves as a principal food source for the aquatic community in the everglades.

Heald (1969) estimated that 95% of the total net production of mangrove leaves in a Florida estuary eventually enter the aquatic system as detritus. Teal (1962) has estimated that 45% of total net production of Spartina enters the estuarine waters in the Georgia coastal marshes.

A. Decomposition and Nutritive Value

The major contributor to the detrital pool in the Barataria Bay estuarine system is Spartina alterniflora; and the ultimate utilization of this primary production by economically important marine organisms is dependent upon decomposition by bacteria, fungi, and microscopic animals.

Several means have been employed in the study of the decomposition and nutritive value of plant material. Teal (1962), working with inoculated Spartina material in the laboratory, found an initial decrease in fat and protein percentages. Fat continued to decline slowly, but protein content increased slowly until at 16 weeks it was

twice the initial concentration. Carbohydrate remained constant, but fiber declined to 1/4 of its initial value.

Burkholder and Bornside (1957) studied the decomposition of Spartina in nature by enclosing shoots of fresh green grass in lath crates which were than submerged in shallow water. Decomposition was slow in winter and rapid in spring and summer. The leaves were rapidly decomposed, but the cellulose and lignin of the stems was not completely broken down after 300 days.

Waits (1967) utilized nylon mesh litter bags to determine the rate of decomposition of marsh grasses. The initial rate of decomposition was rapid even though the bags were placed in the marsh in early winter. The rate declined in the remaining winter months, but increased with warm weather. He attributes the initial high rate to easily decomposed constituents.

Odum and de la Cruz (1967) measured decomposition of Spartina by enclosing dead standing plant material in litter bags which were placed at different tide levels in the marsh. They found that 58% of the plant material was decomposed in 300 days.

Fenchel (1970) found that a detritus-consuming amphipod feeds on detrital particles and on its own fecal pellets, but it only digests the associated microorganisms. The dead plant residue apparently passes undigested through the intestine.

Newell (1965) has gound that the prosobranch Hydrobia ulvae and the bivalve Macoma baltica are unable to utilize the cellulose of detritus particles, but are capable of digesting the adsorbed microorganisms.

Malone and Swartout (1969) working with particulate organic matter in old-field and forest soils found a direct relationship between caloric value and particle size. They attribute the high caloric value of the smaller particle sizes to increased microflora impregnation.

W. E. Odum states that "the omnivorous detritus consumers appear to obtain nutrition primarily from the microorganisms adsorbed upon detritus particles. These microorganisms are able to convert resistant plant tissues such as cellulose and lignin into fungal and bacterial protein which the omnivorous fishes and invertebrates are able to utilize" (1971, p. 147).

Although the importance of detritus to the aquatic food web has been extensively documented, very little evidence is available which describes the actual process or mechanism by which dead grass is converted to microbial mass or consumed prior to total conversion. Several measurements of degradation of whole plant material to large size detritus particles (2mm or more) have been reported; however, little is known about the final conversion. A number of possibilities are proposed, and the entire process of decomposition is discussed in the text of this paper.

MATERIALS AND METHODS

A. Primary Production

The primary net production of streamside and inland marsh areas was determined by taking monthly samples from one-fourth square meter quadrats. Ten randomly chosen samples were collected each month from each of the two sample areas.

The streamside sample area was a rectangular plot one hundred twenty-five meters long by five meters wide; the inland sample area was twenty-five by twenty-five meters square. The boundaries of both areas were delimited prior to sampling, and each consisted of an area large enough to insure that none of the quadrats were resampled. Provisions were also established prior to sampling to insure that trampling of sample quadrats did not occur.

The vegetation was clipped at mud level within the one-fourth square meter frame, and all dead material on the mud surface removed. The bagged vegetation was returned to the laboratory where it was separated into living and dead material and oven-dried at 60C to constant weight. The average monthly standing crop of live and dead material was determined and expressed in grams per square meter.

The caloric content of both live and dead material was determined by bomb calorimetry on one monthly sample from each area in order to express productivity data on an energy basis. Randomly chosen samples of both live and dead oven-dried grass were each ground in a Wiley Mill, and the caloric determinations accomplished with a Parr-Adiabatic Bomb Calorimeter. Initially two determinations were made per sample;

however, this proved time consuming and was reduced to one determination when duplicates were found to vary only slightly.

Color infrared photographs taken by NASA[1] in their March 1971 overflights of the Barataria Bay area were utilized to calculate the areas covered by tall and short Spartina, so that average production per unit area of marsh could be computed. An area near Airplane Lake was selected for this study, as Spartina productivity measurements in the vicinity of the lake had been previously obtained.

Considerable areas of the marsh are either bare or covered with water; therefore, productivity measurements are useless if these non-vegetated areas are not taken into consideration. Vegetation types as well as water and bare spots were easily distinguished on color infrared photographs.

The percentage distribution of water, bare area, and streamside and inland Spartina marsh was determined by a grid method. A grid developed on a plastic transparency was superimposed over a one square mile area of the color infrared photograph and enlarged with an overhead projector. The number of grid crossings or points were counted for each of the four area types encountered, and a percentage distribution determined. From this information and previously collected data on Spartina production, it was possible to calculate the total net production of Spartina per "average" acre of marsh surface.

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[1] Obtained from the Coastal Studies Institute through the cooperation of Dr. William G. Smith.

B. Litterbag Loss

This experiment was designed to measure the rate at which marsh vegetation is reduced to a size small enough to be washed from the marsh surface. This was accomplished by enclosing a known amount of dead standing Spartina in nylon mesh bags with two millimeter holes. The bags were secured and staked out in one of three selected areas. These included the inland marsh sampling area of short Spartina, the streamside sampling area of tall Spartina, and a third in the channel draining Airplane Lake.

The study was conducted twice; the first from July, 1970 to May, 1971, the second was from December, 1970 to June, 1971. The two tests measured the differences in the rate of disappearance between summer and winter months.

A correlation was made at the beginning of the experiment between wet weight and dry weight of the vegetation in order to express sample data on a dry weight basis. Monthly samples were collected and consisted of the removal of three bags from each area. The bags were returned to the laboratory where they were rinsed to remove accumulated silt, and any animals and animal material were separated from the vegetation. The material was then oven dried to constant weight, and the material remaining in the litterbags was expressed as percent remaining per month.

C. Spartina Decomposition

This experiment was designed to examine in some detail the decomposition of Spartina under laboratory conditions. The objectives were to determine (1) the effects of temperature on the rate of

decomposition, (2) the effects of the original particle size on the rate of decomposition, and (3) the nutritive value of the different size fractions.

Oven dried, dead standing Spartina stems and leaves were ground in a Wiley Mill, and four different size fractions obtained by dry sieving through standard soil sieves. The ground material was sieved through successive sieve sizes of 250, 177, 149, 74 and 60 microns. The actual size of the particles was taken to be the median between the largest size sieve passed and the next smaller size by which it was retained. For example, particles passing through the 250 micron sieve and trapped by the 177 micron sieve were considered to be an average of 213 microns in diameter. The other three mean sizes were 163, 111, and 67 microns.

The dry particle sizes were found to increase only slightly when soaked, and were within the range of particle sizes utilized by Fenchel (1970) and Odum and de la Cruz (1963).

Two replications consisting of three grams of ground grass of each of the four particle sizes were placed in liter erlenmeyer flasks. Three hundred milliliters of filtered sea water plus three hundred milliliters of three-fourths strength ASP-2 (Provasoli 1957) were added to each of the flasks. A five milliliter innoculum consisting of finely ground grass and decaying Spartina leaves was added to each flask. All flasks were aerated and each magnetically stirred by a synchronus belt-driven apparatus designed by the author. The pH was adjusted at intervals with a 0.1 molar sodium hydroxide solution. Two-tenths percent ammonium sulfate was added as a nitrogen source on the twentieth day of incubation.

The four particle sizes were incubated at a constant temperature of 30C for four weeks in the dark. Five milliliter aliquots were pipetted from each replicate at approximately three day intervals. Respiration of the samples was measured on a Gilson Respirometer after which the ash-free dry weight of the material of each flask was determined.

Ten milliliter samples were also removed at weekly intervals in order to determine total nitrogen and oxidizable carbon. The material was filtered and washed with 3% ammonium formate to remove soluble salts. Using techniques described by Strickland and Parsons (1968), total nitrogen was determined by a modified Kjeldahl technique and carbon by wet oxidation with dichromate.

Photographs were taken of each particle size fraction at the beginning and at weekly intervals thereafter.

RESULTS AND DISCUSSION

1. Standing Crop

A high rate of primary productivity would be expected in the Louisiana coastal salt marshes due to the favorable growing conditions of a nearly subtropical climate. Production measurements were made by determining the monthly standing crop of live and dead material of both the inland and streamside marsh areas. The data cover a fourteen month period, and included one complete growing season and part of another. An analysis of variance and F-test of the data were computed for both streamside and inland areas (Appendix Table 1). The F-test indicated that a significant variation exists over and above sampling error both in time and between locations. A significant interaction was also found to exist between the area by month values in the dead standing crop. This may be attributed to larger differences between inland and streamside values in winter. All F-values proved to be highly significant. F-values for comparing the effect of different individuals taking the samples were non-significant, and it can be concluded that no difference existed between samplers.

Data presented in Figure 2 indicates that the live standing crop of both the streamside and inland marsh areas was highest in the summer months, but declined rapidly when flowering occurred in late September and October. Low standing crop occurred in the period of December through January with the low in the streamside area being approximately 200 and the inland area 100 grams per square meter.

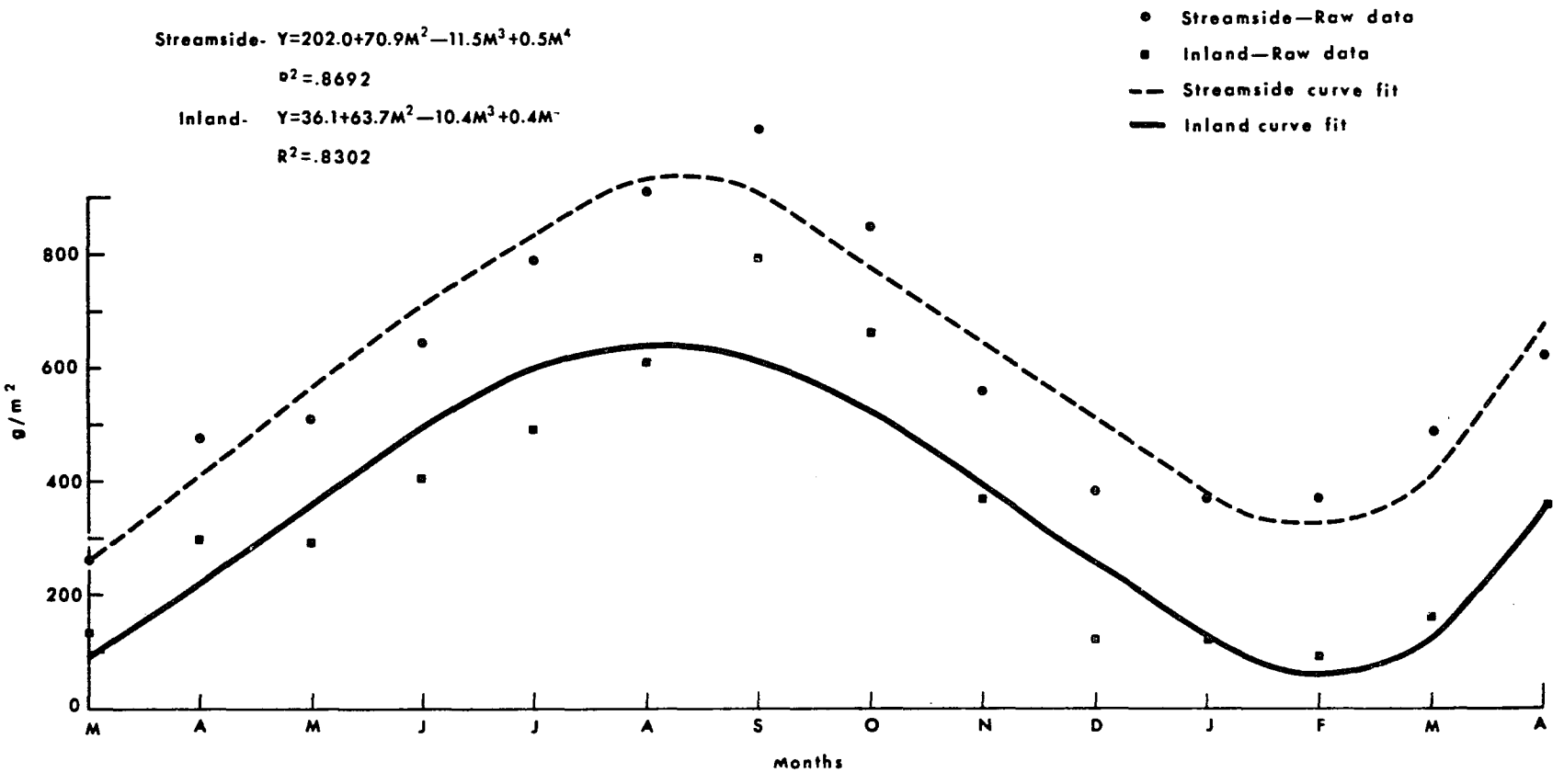


Figure 2. Live standing crop of streamside and inland Spartina expressed as grams per square meter.

The dead standing crop (Figure 2) of both areas was lowest in the summer and highest in the winter months, and was inversely related to live production. Lowest standing crop of dead material was approximately 700 grams per square meter for the inland area and 800 for the streamside which is nearly equal to the live standing crop at the corresponding sample period. This rather large amount of dead material seems to indicate that death of live material is a continuous process even in periods of favorable growing conditions.

Large quantities of dead material have been observed to accumulate on the marsh surface during the winter months, and this is obvious from the data presented in Figure 2. A high rate of death of live grass began after flowering had occurred in October, as seen by the rapid increase in the dead standing crop during this period. The onset of cooler winter temperatures with resulting loss of microbial activity, and the absense of the south winds which drive water up onto the marsh results in a slower loss rate from the marsh surface. Large quantities of dead grass are thus stored on the marsh in winter. This material is washed out rapidly in the spring.

2. Net Production

Net production of Spartina was calculated according to Smalley's method, as described in the Literature Review. This method measures changes in the monthly standing crop of both live and dead material, and is an improvement over the peak standing crop methods which were utilized previously.

Net production of both the streamside (Table 1) and the inland (Table 2) marsh areas was greatest in the spring and summer months,

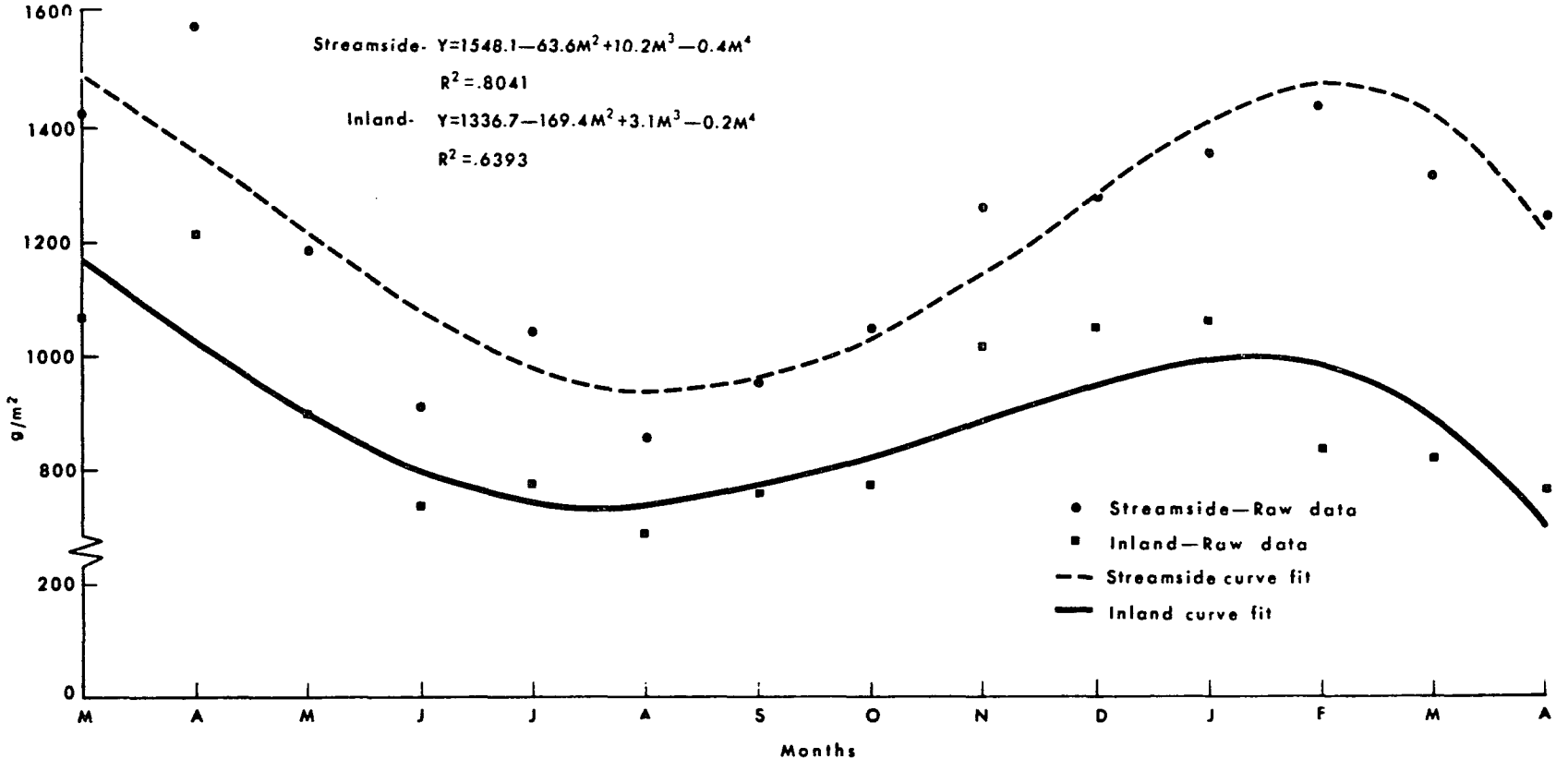


Figure 3. Dead standing crop of streamside and inland Spartina expressed as grams per square meter.

but declined rapidly from October through January. Live standing crop was considerably higher in the spring months of the second year, as 487 g/m^2 occurred in March of 1971 while only 266 g/m^2 was collected in March of 1970. This is attributed primarily to the extremely cold temperatures in the winter and early spring of 1970. It is noteworthy that a substantial quantity of live grass is on the marsh during these winter months, although this method of calculation shows no net production for this time interval.

Total net production of the streamside area amounted to 1409.6 grams per square meter for twelve months while the inland total was 1005.5 grams per square meter. These values are higher than those calculated for the Georgia coastal marshes, and considerably greater than those of the more northerly Atlantic coastal marshes.

Even though net production calculations may be considered high, certain discrepancies are inherent in Smalley's method. For example, little or no production is recorded for the October through January months even though new shoots were observed at all sampling periods. Large quantities of dead grass accumulated on the marsh surface in winter are also not accounted for in the annual total of net production, as much of this material is washed out rapidly between sample periods in the spring.

For these reasons an alternate method is suggested which estimates true net production more closely. It used the method described by Wiegert and Evans (1964) and is discussed in a later section.

Table 1. Calculation of net primary production of streamside marsh according to monthly changes in standing crop. (gm dry wt/ m^2)

Month	Standing Crop		Change		Net Prod.
	Live	Dead	Live	Dead	
March	266.4	1423.3			
			209.5	157.1	
April	475.9	1580.4			366.6
			28.5	-394.8	
May	504.4	1185.6			28.5
			138.8	-278.4	
June	643.2	907.2			138.8
			144.4	134.4	
July	787.6	1041.6			278.8
			112.8	-188.4	
August	900.4	853.2			112.8
			118.0	89.6	
September	1018.4	942.8			207.6
			-169.6	100.0	
October	848.8	1042.8			0.0
			-295.2	212.0	
November	553.6	1254.8			0.0
			-176.4	10.8	
December	377.2	1265.6			0.0
			-13.6	85.2	
January	363.6	1350.8			71.6
			4.4	82.6	
February	369.3	1433.4			87.0
			117.9	-122.6	
March	487.2	1310.8			117.9
				Annual Total	1409.6

Table 2. Net primary production of inland marsh calculated according to monthly changes in standing crop. (gm dry wt/m^2)

Month	Standing Crop		Change		Net Prod.
	Live	Dead	Live	Dead	
March	133.2	1061.9			
			166.6	152.2	
April	299.8	1214.0			318.8
			-10.2	-315.2	
May	289.6	898.8			0.0
			113.2	-163.6	
June	402.8	735.2			113.2
			86.0	34.8	
July	488.8	770.0			120.8
			113.6	-86.4	
August	602.4	683.6			133.6
			185.2	73.6	
September	787.6	757.2			258.8
			-131.6	6.0	
October	656.0	763.2			0.0
			-294.0	248.8	
November	362.0	1012.0			0.0
			-246.8	36.0	
December	115.2	1048.0			0.0
			1.2	6.8	
January	116.4	1054.8			8.0
			-28.7	-220.0	
February	87.7	832.8			0.0
			72.3	-16.8	
March	160.0	816.0			72.3
				Annual Total	1005.5

3. Litterbag Loss

An understanding of the decomposition and loss of dead standing crop in coastal marshes has become important to the comprehension of these ecosystems as a whole. The loss of marsh grass produced to the surrounding waters of the marsh, for example, determines the ultimate availability of this material to the variety of detrital-based consumers. More important to this study, however, is the effect of seasonal variation of loss rates on net primary production.

The litterbag method was selected to measure the loss of dead grass, because it was the best means available. The loss of dead material from the litterbags is a function of several interrelated factors including: (1) the size of the mesh of the litterbags, (2) the area in which the material occurs, (3) temperature, and (4) the amount of tidal flushing which occurs.

Dead standing Spartina enclosed in the litterbags and set out in June 1970 are referred to in this study as year one and those set out in the following January as year two. Analysis of variance of the data is presented in Appendix Table 2. The F-values indicate that a highly significant variation exists above sampling error due to differences both in area and month sampled. A highly significant difference was also found to exist between year one and year two sample data.

Data presented in Figures 4, 5, and 6 indicate that material placed in the bags in the summer decomposed and was washed out more rapidly in all three areas than material set out the following January.

The material in the bags must first be decomposed by micro-organisms and possibly benthic invertebrates to a size small enough to

move through the two millimeter mesh of the bags. The rate at which this occurs is primarily a function of temperature. After a minimum critical size is reached by decomposition, tidal flushing is apparently responsible for movement of the particles out of the bags and into the water.

Loss of material from the bags located in the tidal channel draining Airplane Lake (Figure 4) was considerably more rapid than those of the other two areas. Fifty percent of the original material was lost from the bags in fifty days with approximately seventy-five days required for fifty percent removal along the streamside (Figure 5), and 125 days for fifty percent removal in the inland marsh (Figure 6).

Loss in the winter months is considerably slower as indicated by the slope of the line in year two data, and also by slower rates during the winter and early spring of year one data.

It is postulated that the original material placed in the bags was mechanically reduced to smaller particle sizes rather rapidly by the grazing activity of amphipods and other invertebrates. Amphipods were noted to be in abundance in and around the bags, particularly those bags in the stream and along the streamside.

Cellulose decomposers and other related microorganisms are then considered responsible for further reduction in particle size.

4. True Net Production

Calculations of net primary production according to a conventional method such as that of Smalley have not proven accurate, as (1) they do not account for the production of new shoots during periods of rapid decline in mature live standing crop, and (2) they do not account

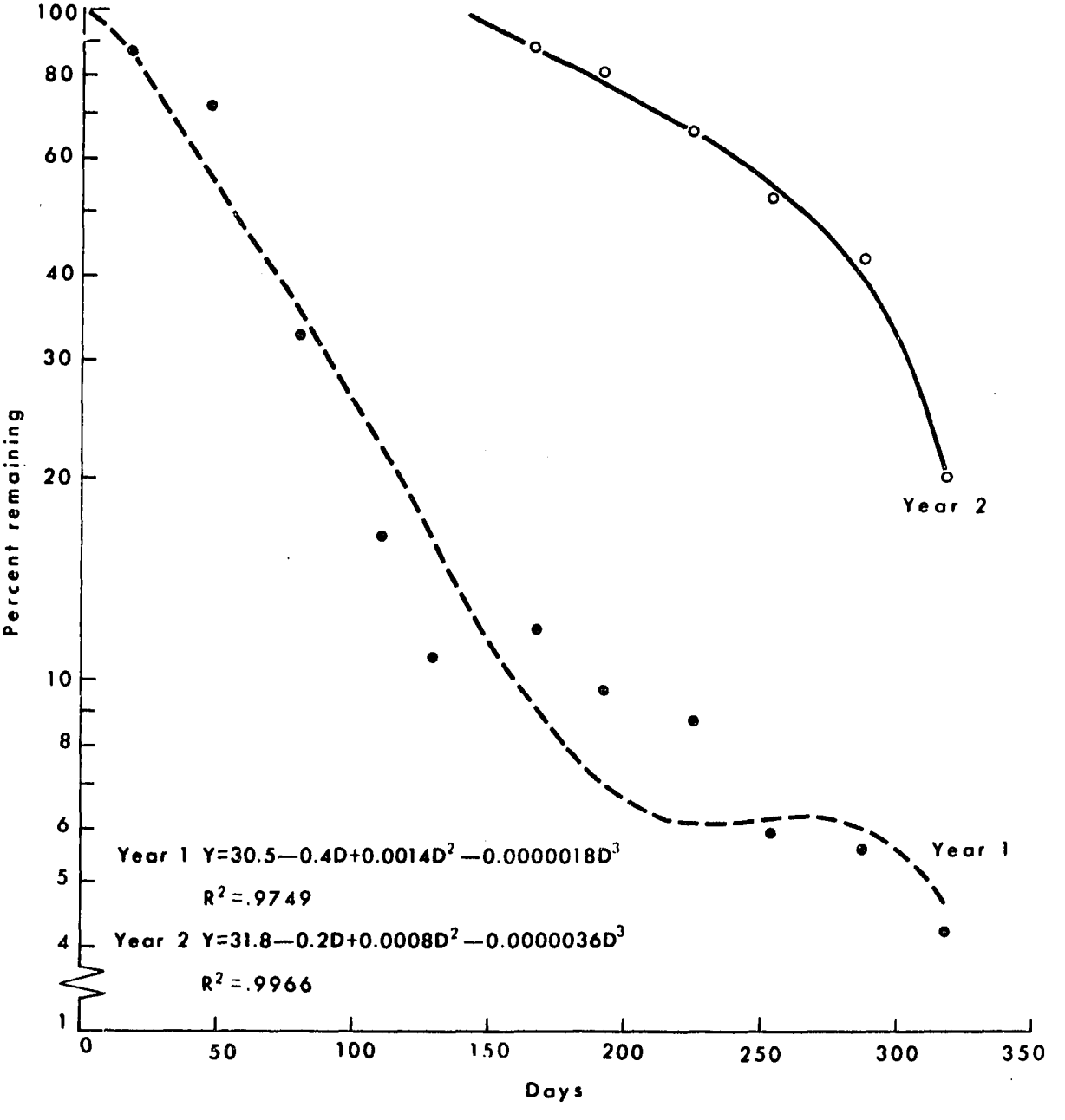


Figure 4. Measurement of the loss of Spartina from nylon mesh litterbags in a tidal stream.

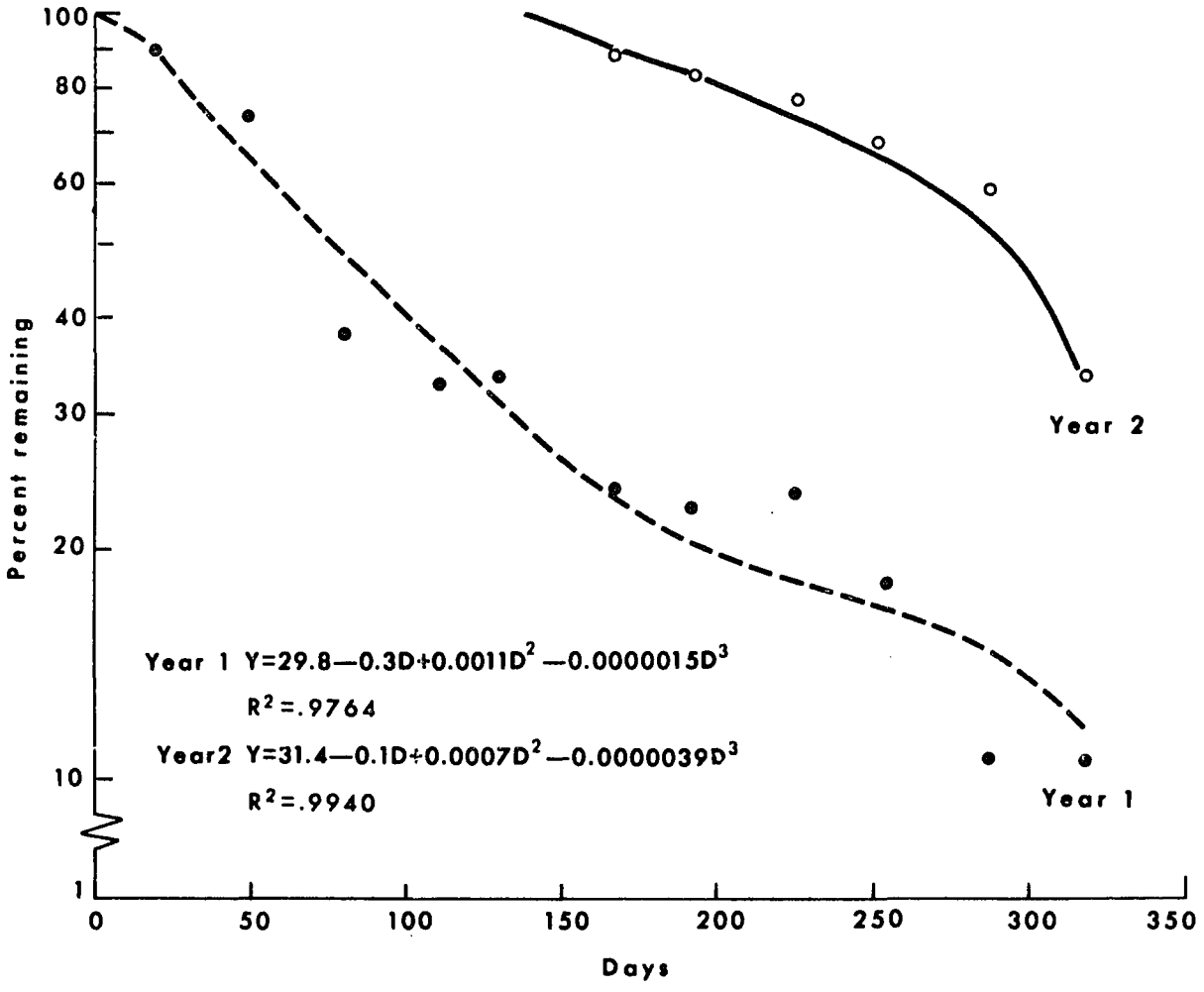


Figure 5. Measurement of the loss of Spartina from nylon mesh litterbags in the streamside marsh.

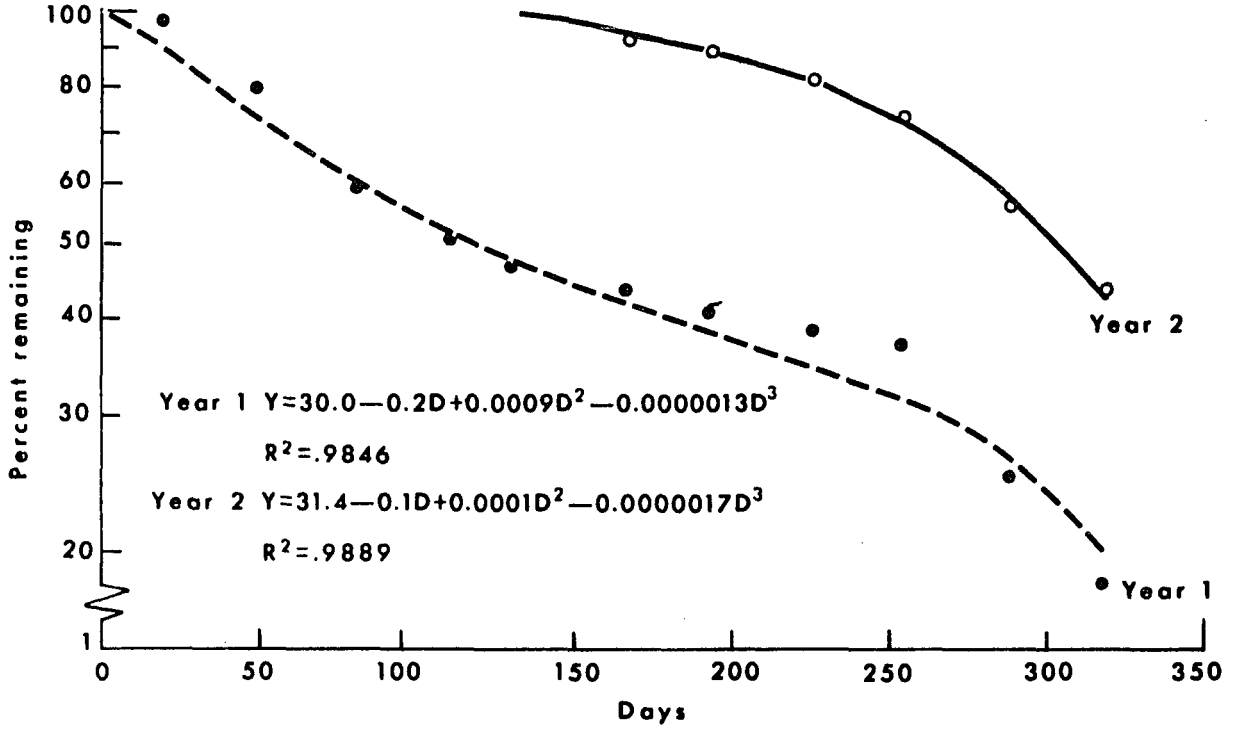


Figure 6. Measurement of the loss of Spartina from nylon mesh litterbags in the inland marsh.

for material lost to breakdown and tidal flushing between sampling periods. The latter discrepancy is most important in salt marsh ecosystems which are subject to constant flushing by tidal inundation.

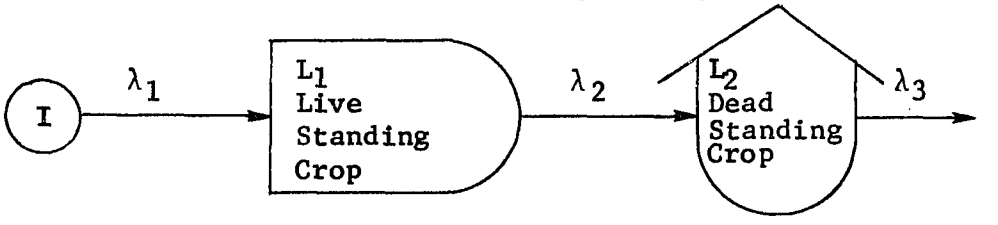
Wiegert and Evans (1964) suggested a method which provides a dynamic analysis of the system as a whole, and which does account for loss between sampling periods. They compared the "paired plots" method and the standard litter bag method for measuring loss in a grassland ecosystem, but found the litter bag method inferior. The paired plots method is most accurate for uniform vegetation types; however, it would not prove feasible in a Spartina salt marsh which normally has a high variation in stand density within a given area. The litterbag method which was found to grossly underestimate disappearance on a prairie by Wiegert and Evans was found to be more suitably adapted for the salt marsh, as the material within the bags is constantly in contact with the surface mud. Tidal flushing also occurs daily during all but the winter months, and theoretically should remove all decomposed material of 2mm or less.

The adaptation of the Wiegert and Evans method utilizes information on (1) seasonal production, (2) seasonal death and storage of dead material on the marsh, and (3) a quantitative estimation of the seasonal rate of movement of material into the water. The utilization of this type of information provides a means by which the true net production of both streamside and inland marsh can be calculated.

Both seasonal production and death of live material were measured according to Smalley's method of changes in standing crop, and were discussed previously. The rate of disappearance of dead grass was measured as a loss from litterbags which were staked out in

the sample area. Figures 4, 5, and 6 indicate that a nearly linear graph is produced when plotting the log of remaining material versus time, and from this an instantaneous loss rate can be calculated for any particular time interval (Table 3).

The scheme which is utilized may be represented as:



Incident radiation trapped by the living Spartina plants is converted to organic material (L_1), with the rate at which conversion occurs (true production) being represented as λ_1. The mortality rate of the live material or input into the dead standing crop (L_2) is represented as λ_2, and λ_3 represents the rate of loss of dead material to the water. The change in biomass in a compartment (L_n) per unit time depends on the input of organic matter (λ_n) and loss of organic matter (λ_{n+1}) during that time period. Therefore, true production to a compartment is equal to the change in standing crop in the compartment plus the loss of material from the compartment during that time interval.

$$\lambda_n = \Delta L_n + \lambda_{n+1}$$

Wiegert and Evans show that if the loss of dead material (λ_3) can be measured then the death of live material is equal to the change in standing crop of dead material plus the loss to the water in this time interval.

$$\lambda_2 = \Delta L_2 + \lambda_3$$

True net production is thus equal to the change in standing crop of living material plus the mortality of the live material in that time interval.

$$\lambda_1 = \Delta L_1 + \lambda_2$$

The first parameter calculated was the rate of loss to the water (λ_3) which was calculated from the instantaneous loss rate on a monthly basis (Table 3) times the dead standing crop for the identical time interval. The instantaneous loss rate was calculated as the amount of material lost from the litterbag at the end of each monthly period relative to the amount of material in the bag at the beginning of the monthly period. Loss rates were averaged for year 1 and year 2 in which data was collected for corresponding months. Instantaneous loss rates for the months of June and July were estimated mathematically due to lack of litterbag loss data for the latter two months of the curve. July data was taken from an extension of the curve fit and August data was assumed to be identical to that of August data from year 1.

It was noted from visual observations that considerable quantities of dead grass were piled up on the marsh surface in the winter months; however, with the onset of southerly winds in the spring and consequently higher wind tides, most of the dead material was lost from the marsh rapidly. This is evident from the graph of loss rate data (Figure 7), as a peak in the rate of loss from the marsh is reached in the spring months.

With the instantaneous loss rates determined from litterbag loss plus the change in dead standing crop, a true rate of dead Spartina

Table 3. Monthly instantaneous loss rate calculated from litterbag loss as proportion of mass at beginning of month. (gram lost/gram/month)

Month	Streamside	Inland	Stream
August	.2537	.1842	.3240
September	.2558	.1695	.3543
October	.2480	.1485	.3837
November	.2257	.1238	.4061
December	.1869	.1000	.3796
January	.1127	.0686	.2016
February	.0864	.0720	.0966
March	.0853	.0918	.1014
April	.1228	.1339	.0985
May	.2190	.2136	.2376
June	.4392[1]	.3756[1]	.6210
July	.3465[2]	.2799[2]	.4725

[1] Obtained from an extension of the curve fit.

[2] Obtained from August data.

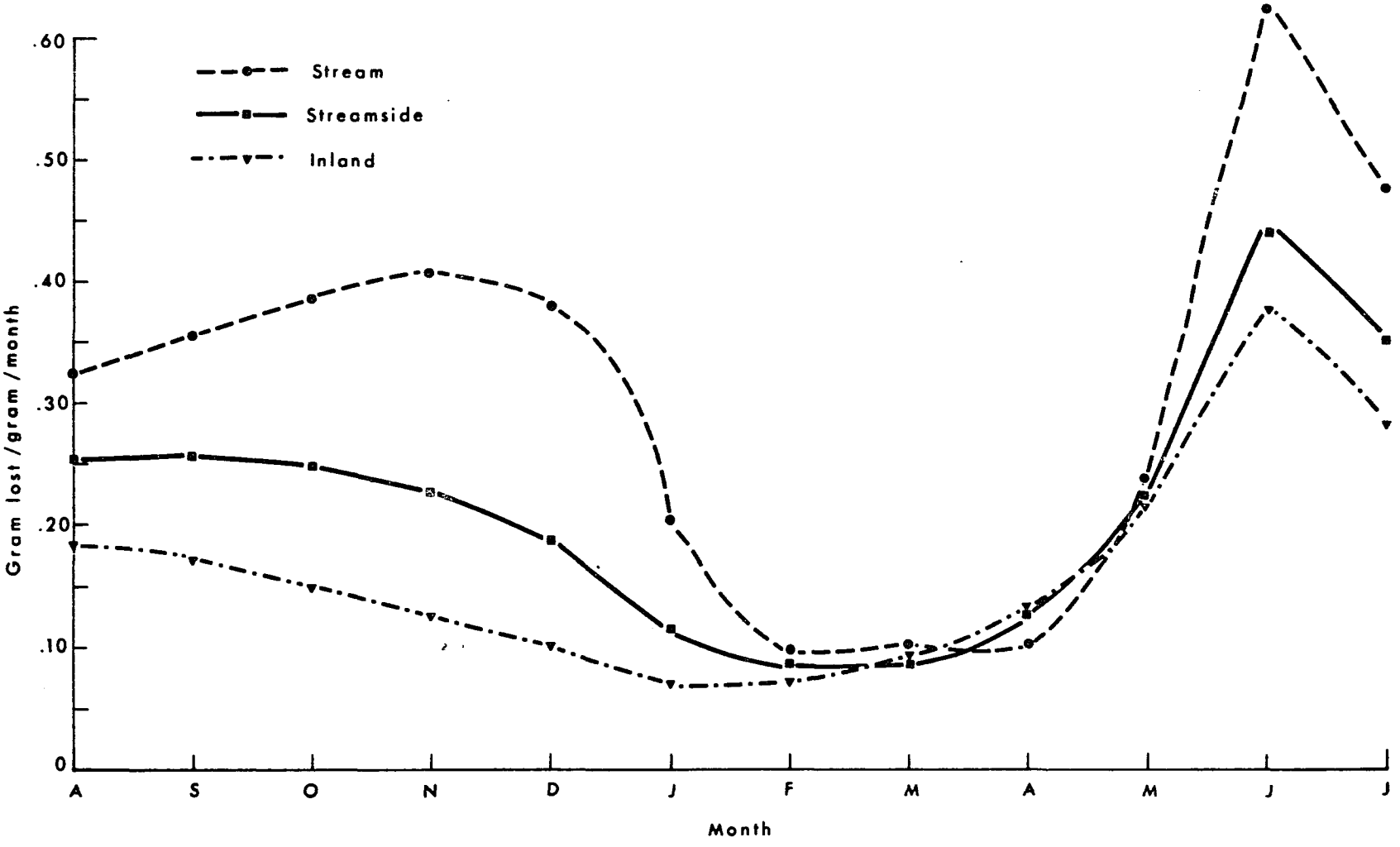


Figure 7. Monthly instantaneous loss rates calculated from litterbag loss for stream, streamside, and inland marsh.

production or mortality rate of live material was calculated (λ_2). Finally with the known rate of input of live material into the dead compartment plus previously collected data on change in live standing crop, the true rate of production of live material was computed (λ_1). All calculations were made from the curve fit data of monthly changes in standing crop and litterbag loss with the intermediate calculation presented in Appendix Table 3.

Figure 8 indicates that the rate of true net production was highest in the spring months with a peak in June, after which it decreased and became constant in the summer and fall months.

Table 4 compares net production computed as a change in the live and dead standing crop, and true net production as adapted from Wiegert and Evans. The true net production is approximately double that obtained by measuring changes in monthly standing crops. True net production monthly values do not necessarily exceed those of changes in standing crop, and it is noteworthy that the true net production values are greater in early spring. This indicates that dead material from the fall die-off, which has remained on the marsh due to lower winter temperatures and low tides, is moved into the water rapidly through tidal flushing in the early spring.

Net production calculations by either peak standing crop determinations or changes in monthly standing crop underestimate the calculated true net production, as these methods do not account for material that is lost either before peak standing crop is reached or between monthly sampling periods. For these reasons the method of Wiegert and Evans has been employed in computing a true net production

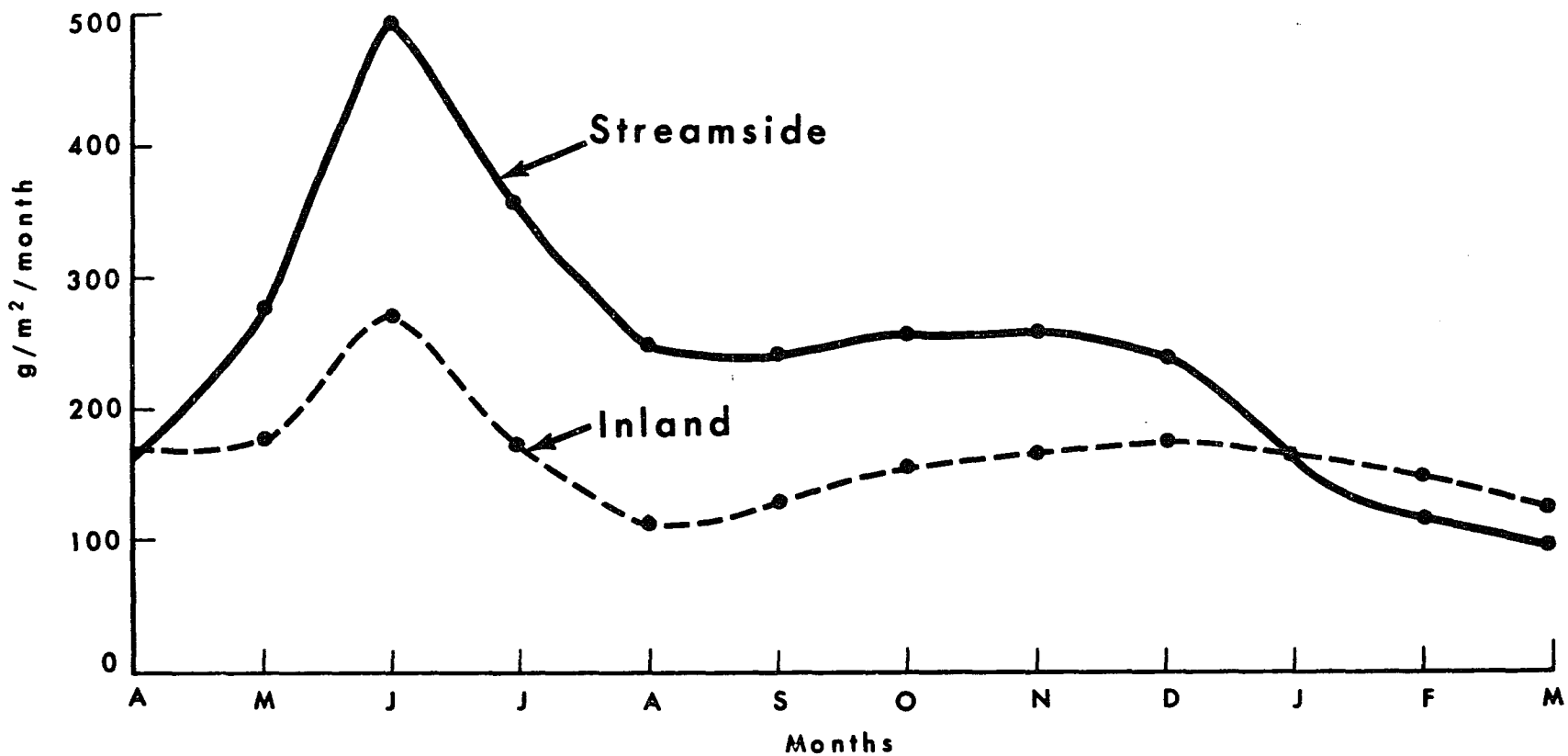


Figure 8. Monthly rate of true net production for streamside and inland marsh.

Table 4. Comparison of net primary production in grams/m^2 of change in live and dead standing crop and true net production.

Month	Streamside		Inland	
	Standing Crop Change	True Net Production	Standing Crop Change	True Net Production
April	336.6	162.0	318.0	173.0
May	28.5	267.5	0.0	179.7
June	138.8	491.1	113.2	273.2
July	278.8	348.0	120.8	173.3
August	112.8	240.2	113.6	110.2
September	207.6	244.6	258.8	128.2
October	0.0	253.3	0.0	149.9
November	0.0	255.1	0.0	167.3
December	0.0	235.5	0.0	175.2
January	71.6	154.2	8.0	157.3
February	87.0	113.9	0.0	148.8
March	117.9	91.6	72.3	124.3
Annual Total	1409.6	2857.0	1005.5	1960.5

which does account for these discrepancies; thus my production figures are considerably higher and certainly more realistic.

5. Caloric Values

Caloric values were determined on a randomly chosen monthly sample of oven-dried live and dead grass from both streamside and inland sample areas. Monthly samples were utilized in order to determine the possible existence of seasonal variations in caloric values; however, only slight differences occurred between months, and seasonal trends were not indicated. Values between areas were also found to vary only slightly; therefore, the monthly determinations of both streamside and inland live, and of streamside and inland dead grass were averaged. The live material averaged 4094 gram-calories per gram dry weight, and the dead 3884.

These values were nearly identical to those of both Smalley (1958) and Stroud and Cooper (1968). The average caloric value of live material was utilized to compute annual net production on an energy basis for both methods of calculating production (Table 5).

Table 5. The annual net primary production in kilocalories per square meter calculated according to changes in live and dead standing crop and true net production.

	Standing Crop Change	True Net Production
Streamside	5,771	11,697
Inland	4,116	8,026

6. Percent Distribution of Marsh Area

The percent distribution of the watershed area surrounding the Airplane Lake marsh was determined according to methods previously specified. Table 6 indicates that approximately 40% of the marsh surface is covered by inland Spartina and nearly 14% by streamside Spartina.

Table 6. The percent distribution of the watershed area surrounding the Airplane Lake marsh as computed from grid points.

Count Number	Number of Grid Points: Inland Spartina	Streamside Spartina	Bare Area	Water	Total
1	96	44	56	75	271
2	112	32	59	68	271
3	119	35	60	57	271
Means	109.0	37.0	58.3	66.7	
% Distribution	40.2	13.7	21.5	24.6	

With available data of annual net production of inland and streamside areas plus the percentage of marsh surface which each type covered, the total net production of Spartina per acre of marsh was calculated (Table 7).

Table 7. Calculations of net primary production on a whole marsh basis, according to changes in live and dead standing crop and true net production.

	Grams/Acre		Lbs./Acre	
	Standing Crop Change	True Net Production	Standing Crop Change	True Net Production
Streamside	778,674	1,578,229	1,715	3,476
Inland	1,636,633	3,191,068	3,605	7,029
Total	2,415,307	4,779,298	5,320	10,505

Considering the percentage distribution of inland and streamside areas plus the change in live standing crop of each, total net primary production per average square meter of marsh surface is 2444 kcal per year. This is nearly 1000 kcal/m^2 greater than the North Carolina salt marshes as reported by Stroud and Cooper (1968). Calculated as true net production, the production per square meter becomes 4848 kcal per year or essentially double that calculated by changes in live and dead standing crop.

7. Spartina Detritus Decomposition

The process by which dead standing Spartina is converted to pariculate detritus and finally into microbial biomass is not clearly understood. A number of different processes are evidently involved with several different biological and physical factors concerned. In situ conditions essentially involve the initial decomposition and breakage of the stem at the mud interface, and this has been substantiated by Meyers (1971) who suggests the formation of a mass of fungal mycelia between leaf sheaths.

Once on the marsh surface it is speculated that further decomposition may be attributed to simultaneous physical and biological factors. Zieman (1968) found that alternate wetting and drying of Thallasia leaves caused the cuticle to shrink and crack. This would also be expected of dead Spartina on the surface of coastal marshes which are subject to alternate wetting and drying by daily tidal inundation. Cracking of the cuticle and epidermal layers of both stems and leaves would facilitate the rapid entry of fungi and bacteria.

A number of microfauna, particularly amphipods, are suspected of playing an important role in the reduction of whole plant material to particulate detritus, but the means by which this is accomplished is not known. It may simply be mechanical or may involve the actual utilization of the plant cellulose by these microfauna (Johannes and Satomi 1966, and Odum 1969). Photodegradation might also be involved to some extent, but nothing has been found to substantiate this.

A. Detritus Decomposition at 30C

This experiment was designed to examine the detailed decomposition of particulate Spartina detritus in the laboratory with the possibility of extrapolation of the results to field conditions. Four particle sizes were chosen which were considered to be small enough to be easily washed from the marsh surface, so that further decomposition would occur in the streams and lakes of the marsh. This work attempted to establish a relation between initial particle size and the rate of decomposition as a result of microfloral activity. An analysis of variance and F-test of the data were computed with the information presented in Appendix Table 4. The experiment was conducted at 30C which is approximately two to four degrees lower than the maximum

spring and summer water temperatures in the marsh. A 0.1 M solution of NaH_2PO_4 was used to buffer the pH.

1. Respiration and Ash-free Dry Weight

Sampling to measure respiration and ash-free dry weight were attempted at four-day intervals, but some samples were lost due to malfunctions of the respirometer.

Data presented in Table 8 indicates that respiration increased with time and decreasing particle size; the ash-free dry weight (Table 9) decreased with time, also more rapidly with small particle size than large, as would be expected from the respiration rate. This information is illustrated graphically in Figures 9 and 10. The respiration rates of the four particle sizes all increased linearly when plotting oxygen consumption with time, and initial particle size was inversely related to the respiration rate. These results indicate that microbial activity is greatest on the smaller particle size and less on the larger. The ash-free dry weight of the particles decreased with time. The rate of decrease was directly related to particle size. The smaller particle sizes were found to have a lower ash-free dry weight with the curves of the graph being similar in the three smaller particle sizes. The 213 micron size particles exhibited a completely different curve, and this cannot be explained.

2. Carbon and Nitrogen

Data presented in Tables 10 and 11 show changes in the percentage of carbon and nitrogen, respectively, in the four particle sizes during 30 days incubation. The percent carbon was observed to remain nearly constant throughout the experiment; however, if these figures

Table 8. Respiration rates of four size fractions of Spartina expressed as milligrams oxygen consummed per gram ash-free dry weight per hour. (30C)

Particle Size (Microns)	Days			
	4	15	19	22
67	1.73	2.20	2.39	2.44
111	1.37	1.83	1.91	1.93
163	1.25	1.36	1.63	1.55
213	1.16	1.29	1.34	1.38

F values highly significant for both particle size and days.

Table 9. Ash-free dry weight of Spartina incubated at 30C. (mg/5ml)

Particle Size (Microns)	Days			
	4	15	19	22
67	19.8	17.5	15.6	14.5
111	22.8	19.8	17.7	16.3
163	22.9	21.1	18.0	17.2
213	21.2	18.9	18.5	17.6

F values highly significant for both particle size and days.

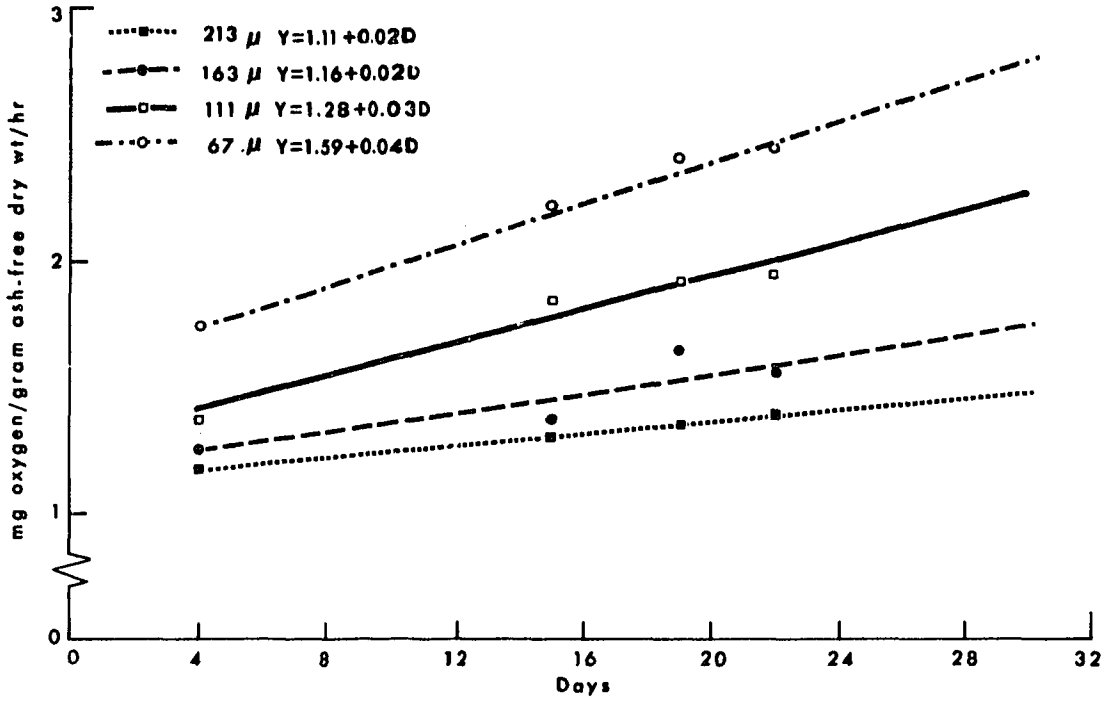


Figure 9. Respiration rates of four particle size fractions of decomposing Spartina.

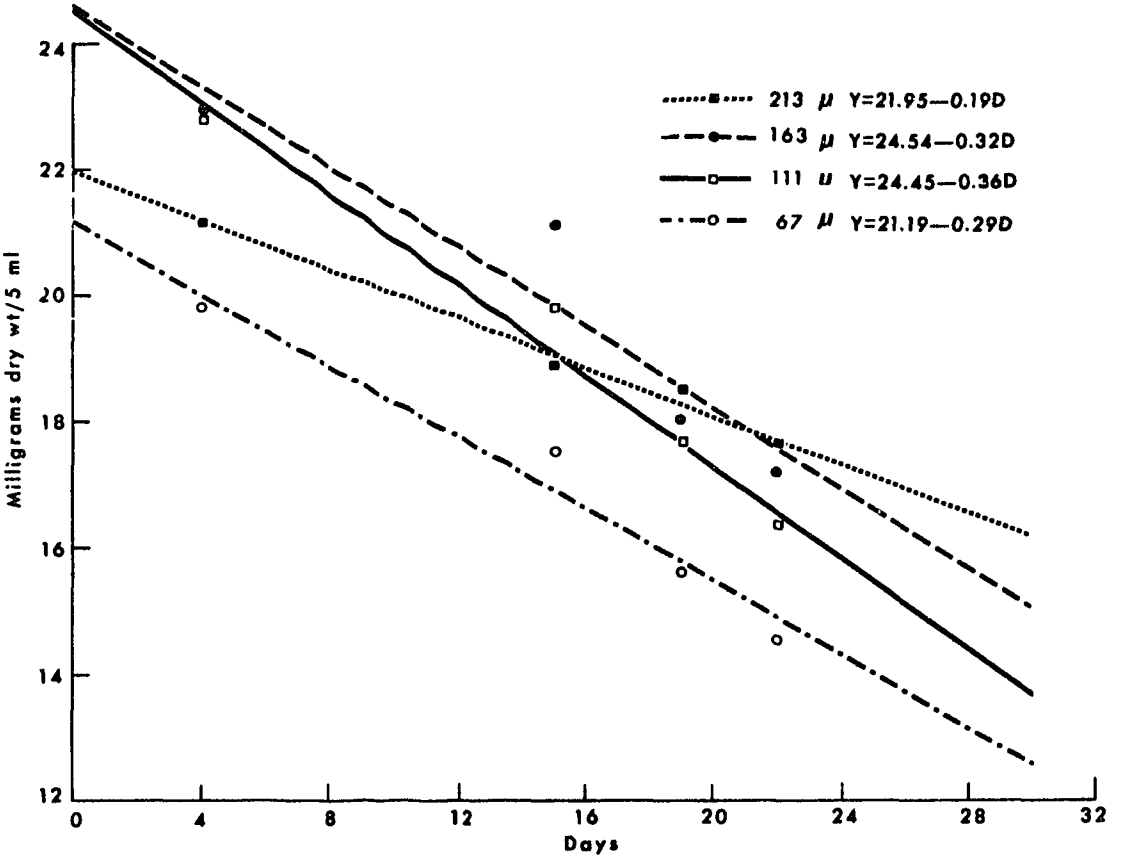


Figure 10. Ash-free dry weight of four particle size fractions of decomposing Spartina.

Table 10. Oxidizable carbon of four size fractions of Spartina expressed in percent of dry weight. (incubation at 30C)

Particle Size (Microns)	Days				
	0	7	15	22	30
67	24.10	25.00	25.46	23.23	23.02
111	25.82	27.87	23.63	24.09	24.62
163	25.20	26.32	20.61	23.20	22.68
213	25.09	25.87	22.51	25.46	22.72

F value for days highly significant.

Table 11. Organic nitrogen of four size fractions expressed in percent of dry weight. (incubation at 30C)

Particle Size (Microns)	Days				
	0	7	15	22	30
67	0.98	3.48	3.98	4.89	8.60
111	0.73	2.43	3.36	3.71	6.84
163	0.59	2.32	3.18	3.06	4.58
213	0.51	1.80	2.19	2.34	3.20

F value highly significant for both particle size and days.

are considered as a percentage of the total dry weight of the aliquot, the percent carbon would decrease with time.

The percent nitrogen was found to be higher initially in the smaller particle size material. This may be due in part to different plant constituents in the different particle sizes. It is speculated that a relatively high amount of leaf material is contained in the smaller size fractions due to easier fractionation of leaf than stem material in the grinding process. The smaller particle size increased from an original 1% to 8.6% total nitrogen in thirty days, whereas the larger increased from 0.5% to 3.2%.

Data presented in Figure 11 indicates that the nitrogen levels of all four particle sizes increased rapidly, but leveled off after one week. The concentrations remained relatively constant until after the third week when ammonium sulfate was added as a nitrogen source on day twenty-one. The percent nitrogen again increased rapidly, particularly with the smaller sized particles. Nitrogen would be expected to become a limiting factor in these small closed systems, and the addition of the ammonium sulfate shows this.

The 8.6% nitrogen of the 67 micron particle size is considered to be nearly total bacterial nitrogen, as Lipinsky and Litchfield (1970) have found that pure bacterial cells contain from 8 to 11% nitrogen depending on the species involved.

3. Microbial Conversion of Spartina

The importance of the detritus particle to the consumer organism is assumed to be restricted to the amount of bacteria or fungi which can be removed from the particle (Fenchel 1971, Newell 1965, and Odum 1971). The rate at which detrital carbon is utilized and nitrogen

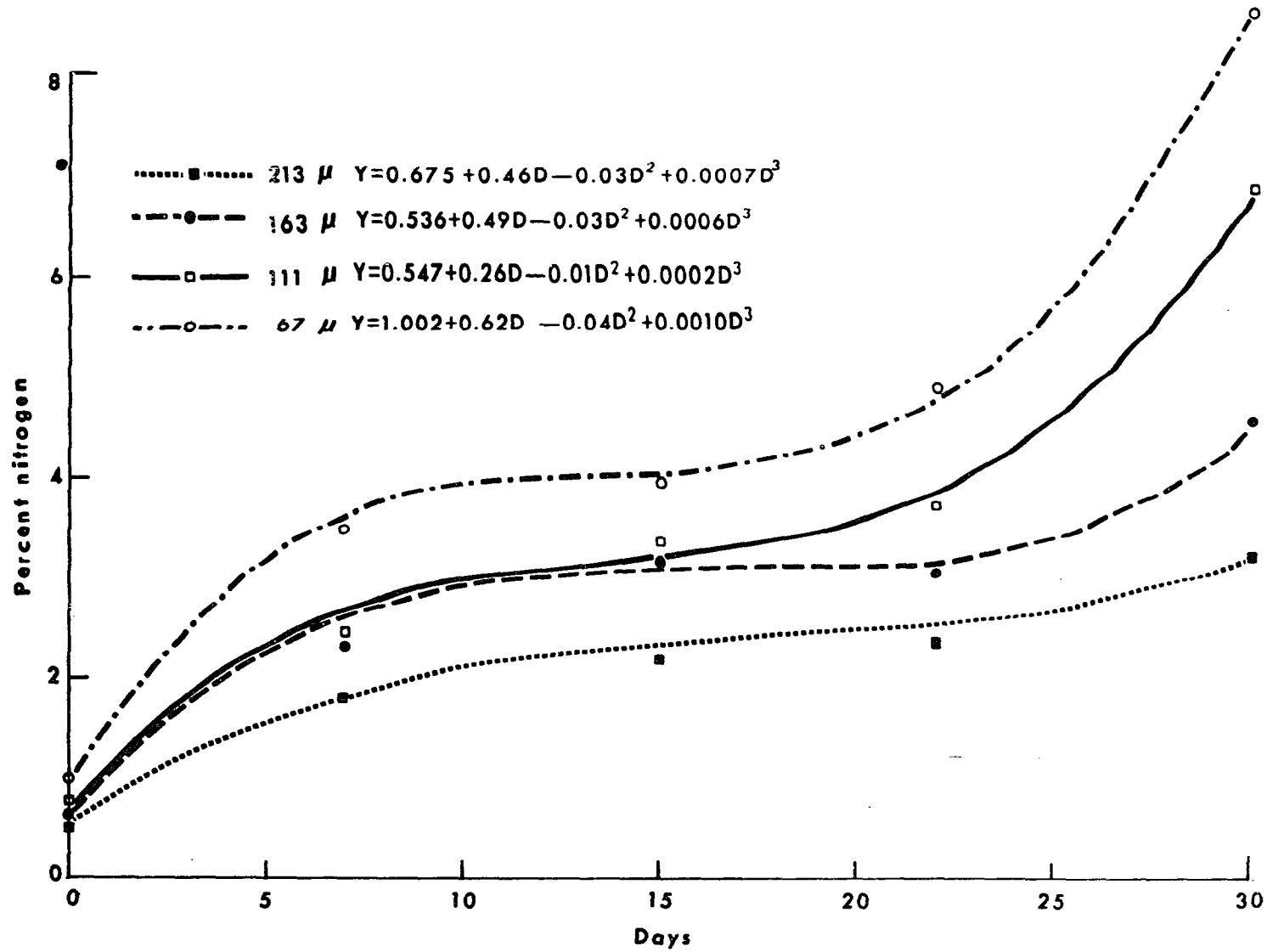


Figure 11. Nitrogen concentration of the four particle size fractions of decomposing Spartina.

converted biochemically into microbial cells thus becomes an important step in the utilization of Spartina by consumers.

The decomposition rate of Spartina and the increase in the bacterial population can be followed by solving simultaneous equations, showing the relationship of particle size to microbial conversion. The equations are:

1. The conservation of mass

$$C_{s+b} = C_s + C_b$$

where:

C_{s+b} = mas/volume of the detrital culture

C_s = mass/volume of Spartina

C_b = mass/volume of bacteria

2. The conservation of organic nitrogen

$$N_{s+b} \cdot C_{s+b} = N_b C_b + N_s C_s$$

where:

N_{s+b} = percent nitrogen in detrital culture

N_s = percent nitrogen in Spartina

N_b = percent nitrogen in bacteria

An average value for N_b of 9% was taken from the literature (Lipinsky and Litchfield 1970), and was assumed to hold for the mixed microbial population of the detrital cultures. N_s was equated to the values of nitrogen determined in the initial analysis of the Spartina fractions (the day 0 column in Table 11). C_{s+b} and N_{s+b} were determined at intervals and the two equations solved for C_s and C_b.

The calculated values are presented in Appendix Table 5 and are illustrated graphically in Figures 12 and 13 in which the loss in Spartina parallels the gain in bacteria. It is also noteworthy that a direct relationship exists between particle size and the rate of conversion to bacterial biomass with the smaller particle size being converted more rapidly than the larger. The 67 micron detrital particles are almost completely converted to bacterial biomass at thirty days while those of 213 micron size are only half converted.

4. Photographs

Photographs were taken of the four size fractions at the beginning of the experiment and at weekly intervals thereafter (Figures 14 and 15). Both the 213 and 163 micron sizes show relatively little decomposition at the end of four weeks; however, on close examination the broken ends of the larger particles exhibit visible breakdown of cell structure, and bacterial "clumping" is obvious. This is particularly obvious in weeks three and four on the 163 micron particles. Decomposition of larger particles and whole plant material apparently begins at the broken ends and progresses along the vertical axis. This was also evident in material collected from the litterbags in which the soft pith of the stems was completely decomposed within several weeks.

Decomposition of the 111 and 67 micron particles occurs rapidly with little cellular detail remaining after three weeks in the 67 micron size. Cellular detail is lost in nearly all 111 micron particles by the end of the fourth week, and very few visibly intact cells remain in the 67 micron particles.

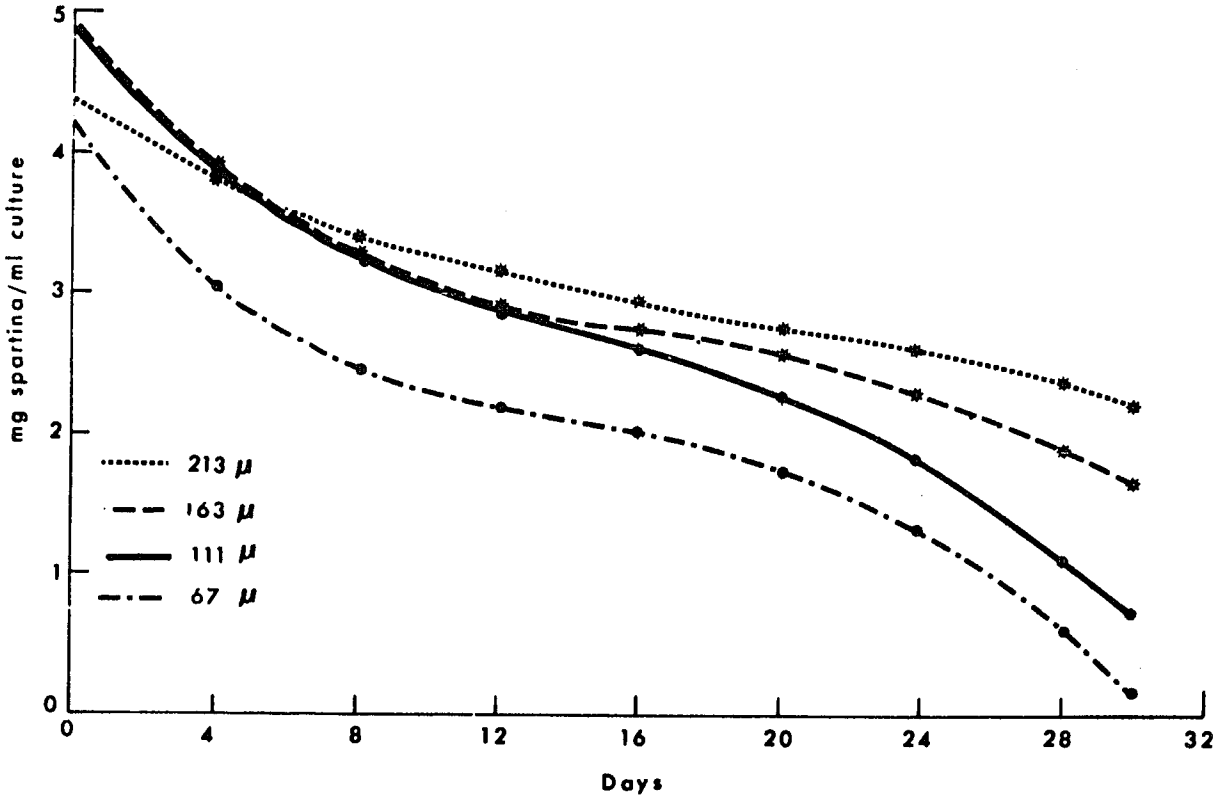


Figure 12. Concentration of Spartina in decomposing culture expressed as ash-free dry weight.

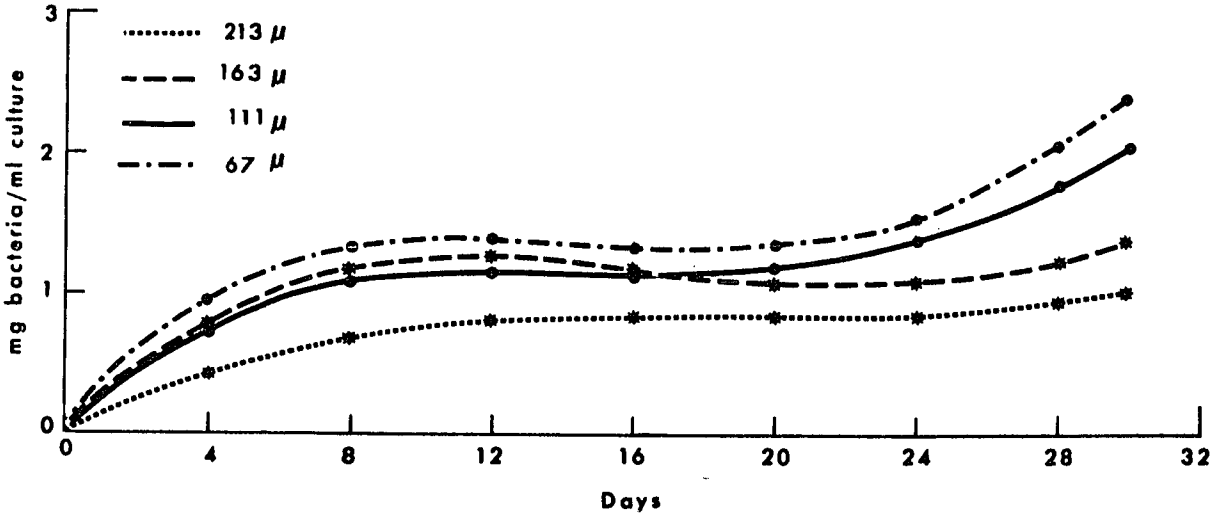


Figure 13. Concentration of bacteria in decomposing culture expressed as ash-free dry weight.

Figure 14. Particle size fractions of 213 microns (A) and 163 microns (B). 0, 2, 3, 4 - length of incubation in weeks.

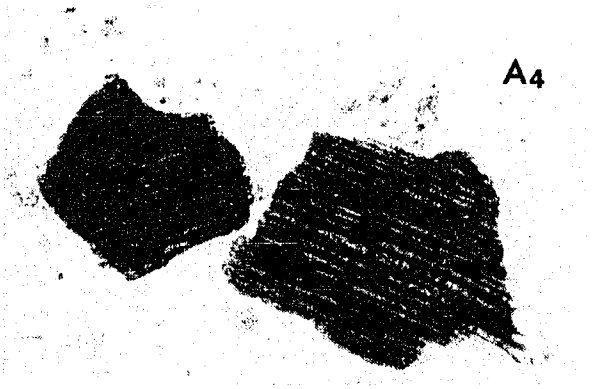

A0


B0


B2


A3


B3


A4

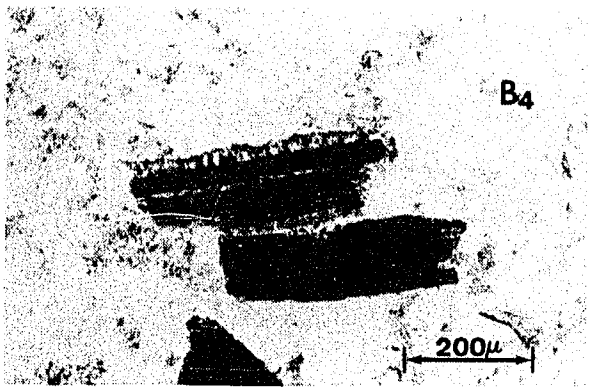
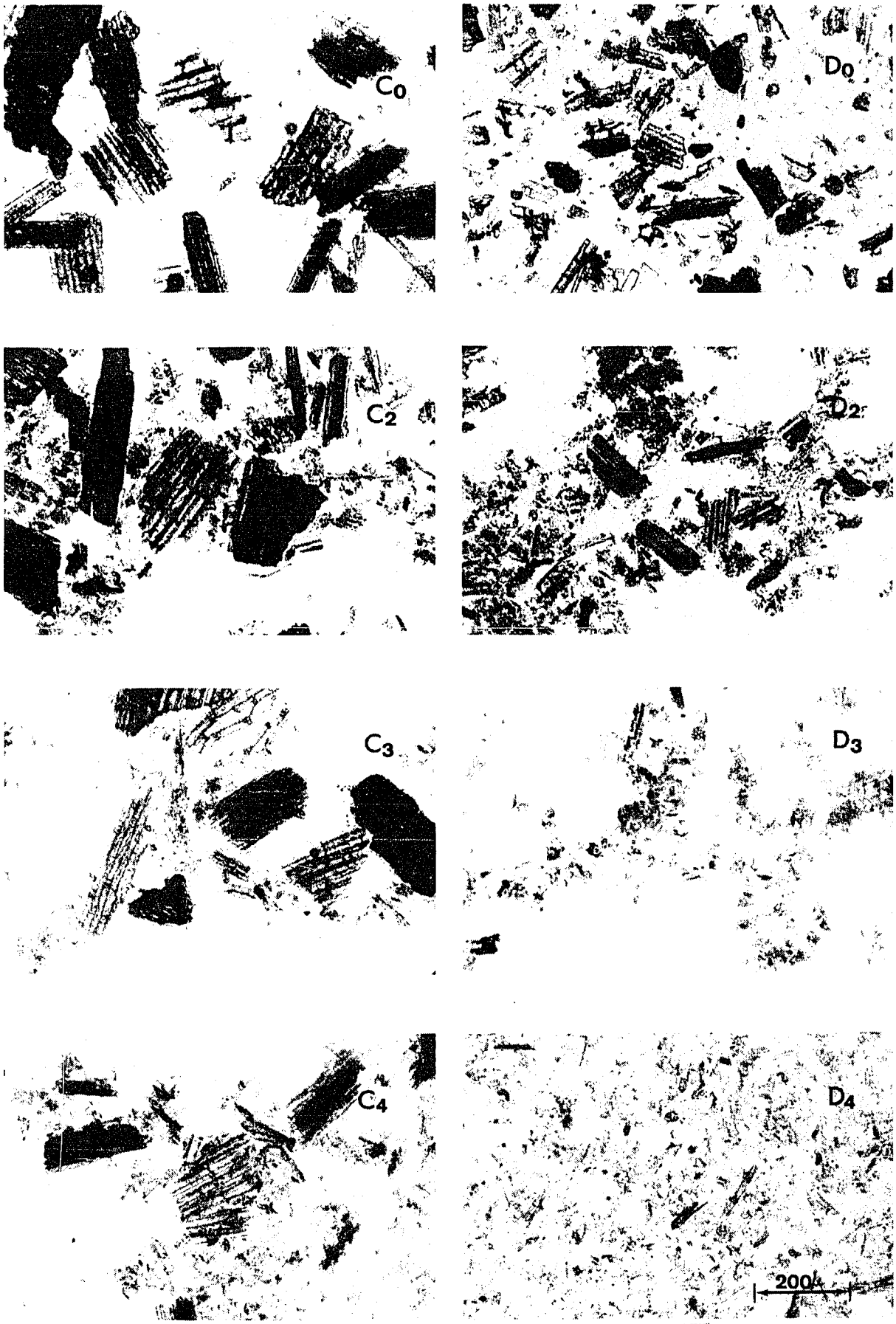

B4
200μ

Figure 15. Particle size fractions of 111 microns (C) and 67 microns (D). 0, 2, 3, 4 - length of incubation in weeks.


C0
D0
C2
D2
C3
D3
C4
D4
200Å

It is evident from these photographs that microbial decomposition is rapid once a minimum critical particle size is reached, and this evidently occurs in the range of 111-67 microns.

SUMMARY AND CONCLUSIONS

The net primary production and decomposition of Spartina alterniflora was studied under both field and laboratory conditions in order to assess (1) net production relative to other coastal marshes, (2) the movement of dead standing crop as coarse detritus into the surrounding marsh waters, and (3) the rate of decomposition of particles which under in situ conditions would be in adjacent marsh waters. The annual net production of Spartina was calculated by two different methods from monthly standing crop data, and the rates of movement of dead material and further decomposition determined by use of litterbags and under laboratory conditions.

Net primary production of both inland and streamside marsh was initially calculated according to a method described by Smalley (1959) which essentially measured the changes in monthly standing crop of live and dead material. This method has been utilized in computing production in several Atlantic coastal marshes, and is considered to be superior to methods which only measure peak standing crop. Productivity in the Barataria Bay marsh was found to exceed all measurements reported for the Atlantic coastal marshes.

Although production was considered high in the Barataria Bay marsh, inherent discrepancies were noted when utilizing the change in standing crop method. Field observations and the standing crop data indicated that considerable quantities of both live and dead material were not being accounted for as shown by the production of new shoots during periods of rapid decline in mature live standing crop, and by

measurements of material lost to decomposition and tidal flushing between sampling periods. For these reasons an alternate method of calculation described by Wiegert and Evans (1964) was used. This method estimates net primary production by summation of changes in standing crop and disappearance and mortality during the sampling period. Information is utilized on (1) seasonal production, (2) seasonal death and storage of dead material on the marsh, and (3) a quantitative estimation of the seasonal rate of movement of material into the water. Utilization of the Wiegert and Evans method increased previously calculated production values by approximately 100 percent. The reliability of this method is felt to be considerably greater than that using changes in standing crop, as it does account for variables not included in the latter method.

The value of this method is its adaptability to use with previously acquired information. The only additional information required besides data on changes in standing crop is the rate of disappearance of dead grass from the marsh. This latter information is available from the literature, as both Odum and de la Cruz (1967) and Waits (1967) have measured the loss of material from litterbags.

The monthly rate of decomposition and disappearance of dead standing Spartina was determined through the use of litterbags for the inland and streamside marsh and for a tidal stream. Bags were placed in the marsh in both summer and winter months to examine temperature effects on the rate of disappearance.

Rate of disappearance from the bags was greatest in the stream, intermediate in the streamside, and least in the inland marsh, and also found to be directly related to temperature. The rate was highest in

the summer months and least in the winter, which supports the observation that quantities of dead material are stored on the marsh surface in winter.

The decomposition and disappearance of Spartina from the marsh surface involve a number of interrelated physical and biological factors. Initial decomposition occurs at the mud interface, resulting in eventual breakage of the stem at this point. It is postulated that much of the initial decomposition of whole plant material is accomplished be amphipods. Bacteria and fungi are suspected of the final reduction in particle size to the molecular level. Tidal flushing is responsible for movement of the particulate detritus out of the litterbags into the surrounding waters of the marsh only after a minimum critical size of less than 2 mm is reached. It is speculated that movement from the bags is analogous to movement from the marsh surface; however, the minimum critical particle size is expected to become increasingly smaller toward the inland marsh. This was obvious in late spring when the streamside area was devoid of any detritus, whereas a "soupy" consistency of fine particles was observed in the inland marsh.

The laboratory study of detritus decomposition included four particle sizes considered to be below the minimum critical size to be carried out of the marsh into the bay water. Under in situ conditions further decomposition would therefore occur in the adjacent waters of the marsh. This study was designed to examine two parameters which included the relationship between initial particle size and the rate of microbial decomposition, and the relative nutritional value of the four particle sizes. Several factors were utilized to measure these

parameters: (1) measurement of respiration rate, ash-free dry weight, percent oxidizable carbon, and percent nitrogen at intervals during incubation at constant temperature, (2) calculation of microbial mass and Spartina mass with incubation with time, and (3) weekly photomicrographs of the four particle sizes to obtain visual evidence of decomposition.

At a constant 30C temperature the data were generally consistent in that the smaller the particle size the more rapid the rate of decomposition. A direct inverse relationship was found between particle size and each parameter measured; the smaller the particle size, the greater the loss in ash-free dry weight and the higher respiration. Similarly, nitrogen was consistently higher in the smaller particle sizes. The rate of increase in microbial mass relative to the decrease of Spartina mass was greater in the smaller particle sizes. The faster decomposition of the smaller particles was obvious in the photomicrographs which indicated that the two smaller size fractions were nearly decomposed after four weeks incubation, whereas very little decomposition occurred in the two larger particle sizes.

It is evident that the minimum critical size in which maximum decomposition rate occurs is in the range of less than 111 microns. Several reasons may be suggested to account for this including (1) high surface area to volume ratio of the smaller particles, (2) relative thinness of the particles allowing rapid and complete microbial penetration, and (3) the possibility that the smaller particle sizes are composed primarily of leaf tissue which might be more easily decomposed than stem tissue.

The nutritive value of the 67 micron particles is considered relatively high, as the percentage nitrogen increased from an initial 1% to approximately 8.5% in four weeks. The conversion rate of the 213 micron particle size was considerably slower, increasing from an initial 0.5% to 3.0% with the other two size fractions intermediate to these two.

From visual observation and experimental evidence a flow diagram (Figure 16) can be constructed which depicts the production and successive stages of Spartina decomposition in the marsh. Several parameters have been measured experimentally, whereas others are only speculation. Monthly values of both live (L_1) and dead (L_2) standing crop were determined, and the rate of disappearance of dead standing crop (λ_3) to small detritus was measured as litterbag loss. From this information the production of live material (λ_1) was calculated.

A combination of the physical and biological factors discussed previously is thought to be responsible for breakage of the dead plants at the mud interface and their eventual degradation to detritus small enough to be washed off the marsh surface. Amphipods, a variety of microflora, and winds and tides are suspected of being primary factors.

Microbial decomposition and consequent enrichment of the particles is completed in the surrounding waters of the marsh. Preliminary measurements of this process were attempted in the laboratory with the information represented as λ_4. Based on these data, in the spring and summer months with a water temperature of nearly 30 degrees, particles within the range of 111 microns or less would undergo complete microbial conversion in approximately four weeks. Larger particles would require successively more time; however, consumer

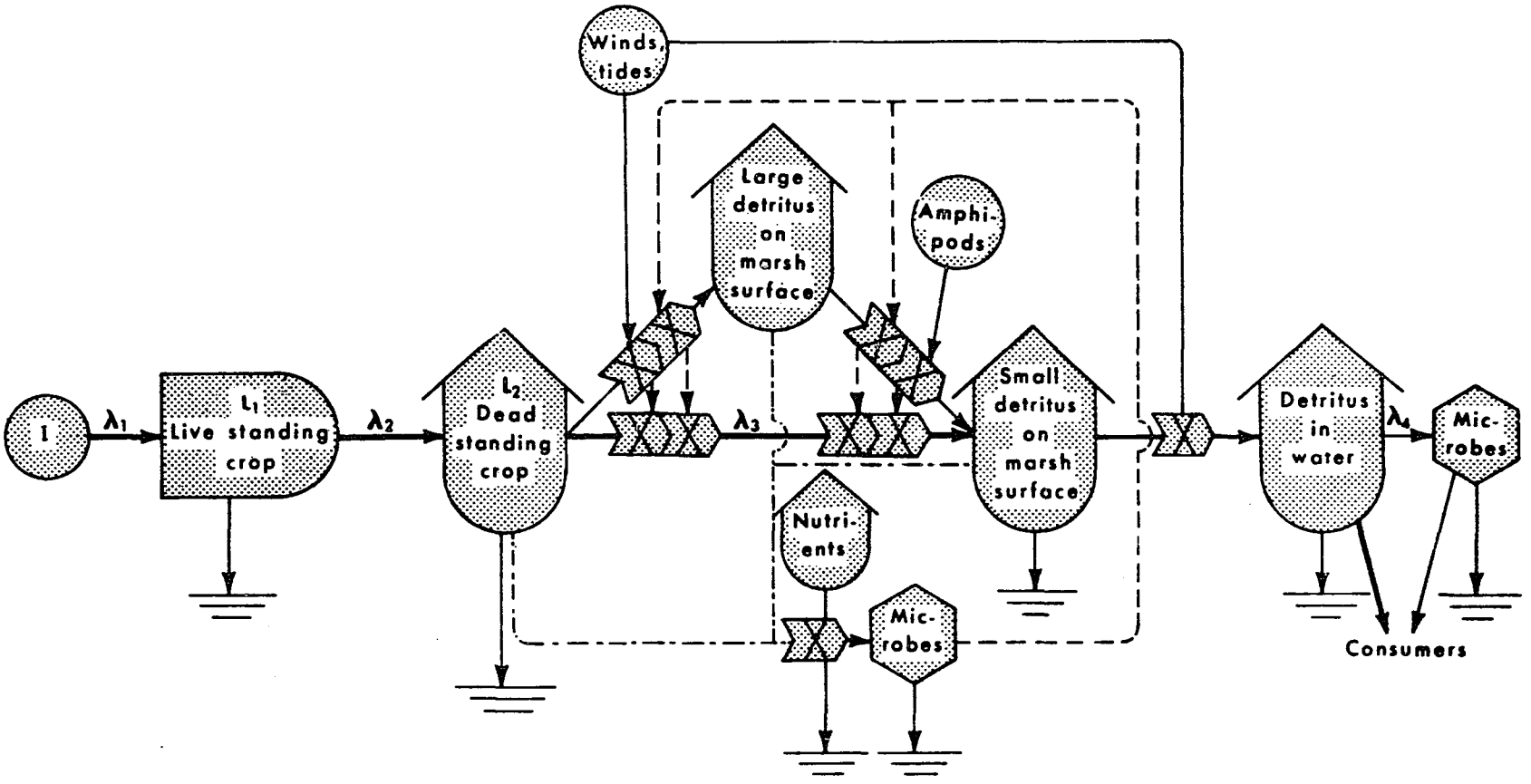


Figure 16. Flow diagram of the production and decomposition of Spartina indicating four measured parameters. Heavy arrows depict major route of flow.

organisms may shorten this time by ingestion of the particles and digestion of the associated microflora. Although the cellulose of the particle is not used by consumers, mechanical fragmentation does occur (Fenchel 1970). Moreover, the finer particles in the fecal material rapidly undergo microbial enrichment and subsequent reingestion by consumers is repeated.

The actual process by which the particle is completely converted to microbial biomass after movement into the water is a complex process with the rate dependent upon a number of factors. A complete understanding of the process can be gained only through detailed experiments closely correlated with studies of environmental variables such as temperature and tides.

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APPENDIX

Appendix Table 1. Analysis of variance of Spartina production.

Source	D.F.	Sum of Squares	Mean Square	F
Live Standing Crop				
Area	1	248657.62	248657.62	244.91**
Month	13	792792.96	60984.07	60.05**
Area x Month	13	11492.07	884.01	0.87
Error	249	252812.65	1015.31	
Dead Standing Crop				
Area	1	294072.23	294072.23	152.69**
Month	13	608255.72	46788.90	24.29**
Area x Month	13	149459.91	11496.92	5.97**
Error	250	481492.98	1925.97	
Live Standing Crop Sampler Interaction				
Area	1	14129.52	14129.52	32.70**
Month	1	20408.56	20408.56	47.24**
Sampler	2	629.47	314.74	0.73
Area x Month	1	243.85	243.85	0.564
Error	32	13825.32	432.04	
Dead Standing Crop Sampler Interaction				
Area	1	80788.09	80788.09	25.63**
Month	1	13934.86	13934.86	4.42
Sampler	2	754.38	377.19	0.12
Area x Month	1	0.30	0.30	0.00
Error	33	104031.86	3152.48	

** Probability at .01 level.

Appendix Table 2. Analysis of variance of litterbag loss.

Source	D.F.	Sum of Squares	Mean Square	F
Litterbag Loss Year 1 Only 11 Months				
Area	2	825.12	812.56	337.69**
Month	10	4790.57	479.06	392.13**
Area x Month	20	149.76	7.49	6.13**
Error	66	80.63	1.22	
Litterbag Loss Year 1 & 2 - 5 Months				
Area	2	4819.50	2409.75	182.56**
Year	1	7394.77	7394.77	560.31**
Month	4	31206.86	7801.71	591.01**
Area x Year	2	358.16	179.08	13.56**
Area x Month	8	1161.31	145.16	10.98**
Area x Year	4	3842.51	960.63	72.77**
Area x Month x Year	8	419.14	52.39	4.00**
Error	60	792.01	13.20	

** Probability at .01 level.

Appendix Table 3. Intermediate calculations of streamside and inland true net production utilizing curve fit data. λ_2 is the change in dead standing crop plus λ_3. λ_3 is the instantaneous loss rate times the mean dead standing crop.

Month	Streamside				Inland			
	Standing Crop				Standing Crop			
	Live	Dead	λ_2	λ_3	Live	Dead	λ_2	λ_3
March	261.8	1494.4			89.7	1170.2		
April	400.8	1369.2	301.0	175.8	214.1	1019.4	297.3	146.6
May	566.9	1218.9	433.7	283.4	361.9	896.4	327.6	204.6
June	719.6	1080.0	643.7	504.8	496.3	809.1	407.7	320.3
July	829.3	979.0	457.7	356.7	590.8	761.0	267.7	219.7
August	878.3	932.4	289.1	242.5	628.9	752.0	148.4	139.4
September	859.8	946.5	226.2	240.3	604.8	777.6	104.1	129.6
October	778.8	1017.8	172.2	243.6	522.8	829.1	67.8	119.3
November	651.3	1132.9	127.6	242.7	397.3	893.9	41.9	106.7
December	505.0	1268.1	89.1	224.4	253.3	955.2	31.2	92.5
January	378.6	1390.0	27.9	149.8	126.0	991.9	30.0	66.8
February	322.5	1455.1	57.9	122.9	60.9	979.2	83.7	71.0
March	398.4	1409.8	167.5	122.2	113.7	887.9	177.1	85.7

Appendix Table 4. Analysis of variance of *Spartina* detritus decomposition.

Source	D.F.	Sum of Squares	Mean Square	F
Respiration				
Particle Size	3	3.68	1.23	109.84**
Error A	4	0.05	0.01	
Days	3	1.02	0.34	25.00**
Size x Day	9	0.22	0.02	1.80
Error B	12	0.16	0.01	
Ash-free Dry Weight				
Particle Size	3	38.20	12.73	18.61**
Error A	4	2.74	0.68	
Days	3	129.80	43.27	86.56**
Size x Day	9	8.37	0.93	1.86
Error B	12	5.96	0.50	
Carbon				
Particle Size	3	28.39	9.46	3.96
Error A	4	9.57	2.39	
Days	4	116.60	29.15	5.88**
Size x Day	12	59.31	4.94	0.97
Error B	16	79.44	4.97	
Nitrogen				
Particle Size	3	61.64	20.55	34.23**
Error A	4	2.42	0.61	
Days	4	216.76	54.19	235.61**
Size x Day	12	34.20	2.85	12.39**
Error B	16	3.69	0.23	

** Probability at .01 level.

Appendix Table 5. The concentration of bacteria in the culture. (milligrams AFDW/ml.)

Days	Particle Size 67μ	111μ	163μ	213μ
1	0.31	0.22	0.23	0.15
4	0.94	0.75	0.80	0.44
8	1.30	1.08	1.17	0.67
12	1.35	1.15	1.24	0.78
16	1.31	1.15	1.18	0.83
20	1.33	1.19	1.10	0.84
24	1.55	1.38	1.11	0.88
28	2.03	1.76	1.26	0.96
30	2.39	2.03	1.41	1.03

The concentration of Spartina in the culture. (milligrams AFDW/ml.)

Days	Particle Size 67μ	111μ	163μ	213μ
1	3.87	4.60	4.61	4.21
4	3.07	3.85	3.85	3.80
8	2.48	3.24	3.24	3.41
12	2.20	2.87	2.91	3.14
16	2.01	2.59	2.72	2.95
20	1.75	2.26	2.54	2.77
24	1.31	1.78	2.28	2.58
28	0.59	1.12	1.88	2.35
30	0.13	0.70	1.16	2.20

VITA

Conrad J. Kirby was born in Opelousas, Louisiana on August 2, 1941. He attended public school in Washington, Louisiana, and graduated from Washington High School in June 1959. He entered the University of Southwestern Louisiana in June 1959 and received a B.S. degree in Botany in January 1964. He received his M.S. in Botany from Louisiana State University in August 1967. He was employed as an Instructor of Biology at Southeastern Louisiana University in Hammond, Louisiana, from September 1967 to June 1970. He married the former Wanda L. Womack in January 1967 and is the father of a 3 year old daughter. He is currently a candidate for the Ph.D. degree in Botany at Louisiana State University.

EXAMINATION AND THESIS REPORT

Candidate: Conrad J. Kirby, Jr.

Major Field: Botany

Title of Thesis: The Annual Net Primary Production and Decomposition of the Salt Marsh Grass Spartina alterniflora Loisel. in the Barataria Bay Estuary of Louisiana

Approved:

James S. Gosselink
Major Professor and Chairman

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Date of Examination:

November 18, 1971